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CONTENTS

Silurian *Hemiarges* (Trilobita) from Cornwallis Island and New York State ..... *H. B. Whittington* 433
The metriophylloid coral genera *Stereolasma, Amplexiphyllum,* and *Stewartophyllum* from the Devonian Hamilton group of New York ..... *Erwin C. Stumm* and *J. Lloyd Watkins* 445
Busycon (Busycon) tritone Conrad redescribed and reillustrated .... *J. A. Fagerstrom* 448
New terebratuloid genera from Australia ..... *Francis G. Stehli* 451
New genera of Upper Paleozoic terebratuloids. ..... *Francis G. Stehli* 457
New genera and subgenera of Jurassic (Bajocian) ammonites from Alaska ..... *Ralph W. Imlay* 467
Orbitolinas from Caribbean Islands ..... *Raymond C. Douglass* 475
Miocene echinoids from the Valle Central, Costa Rica ..... *J. Wyatt Durham* 480
Miocene Foraminifera, mollusks, and a barnacle from the Valle Central, Costa Rica ..... *W. P. Woodring* and *Enrique Malavassi V.* 489
Some Costa Rican larger foraminiferal localities ..... *Enrique Malavassi V.* 498
Muscle attachment impressions in a Cretaceous ammonite ..... *David L. Jones* 502
Actinocamax from the Upper Cretaceous Benton and Niobrara formations of Kansas ..... *J. A. Jeletzky* 505
A new nautiloid, *Eutrephoceras eyerdami,* new species from the Cowlitz formation, upper Eocene, of Washington ..... *Katherine V. W. Palmer* 532
Upper Triassic marine mollusks from the Natchez Pass formation in northwestern Nevada ..... *N. J. Silberling* 535
Some new fossil tortoises from western North America with remarks on the zoogeography and paleoecology of tortoises ..... *Bayard H. Brattstrom* 543
The basicranial articulation of the early Permian cotylosaur, *Captorhinus* ..... *James W. Warren* 561
Stratigraphic implications of a Permian sponge occurrence in the Park City formation of western Wyoming ..... *R. M. Finks, E. L. Yochelson* and *R. P. Sheldon* 564
Major divisions of the Cephalopoda ..... *Rousseau H. Flower* 569
A new species of hadrosaurian dinosaur from the Cretaceous of New Mexico ..... *John H. Ostrom* 575

(Continued on back cover)

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VOLUME 35 MAY, 1961 NUMBER 3

SILURIAN *HEMIARGES* (TRILOBITA) FROM CORNWALLIS ISLAND AND NEW YORK STATE[1]

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ABSTRACT—Neither of the two new species from the Upper Silurian of Cornwallis Island, Northwest Territories, Canada, is represented by a complete specimen, but the disarticulated material of one is silicified. The morphology of the holaspid exoskeleton is revealed in detail, and the development from the late meraspid onward. The second species lacks marginal spines on larger pygidia. Both species are like *H. ptyonurus* from the Upper Silurian of New York State, the original material of which is redescribed. The three species belong to a group of *Hemiarges* species differing in some respects from the type and like species. The distinctive characters of the exoskeleton are combined in so many different ways in *Hemiarges* species, however, that subdivisions of the genus are not now practicable.

INTRODUCTION

DURING the summer of 1959 Mr. Allen R. Ormiston collected parts of trilobite exoskeletons with other fossils from Upper Silurian rocks exposed at Cape Phillips, on the northeastern shore of Cornwallis Island, Northwest Territories, Canada. The trilobite material was submitted to me for study, and I inquired of Dr. R. Thorsteinsson, author of a recent account of the stratigraphy of Cornwallis Island, whether he had obtained any trilobites from Upper Silurian rocks. As a result of my inquiry, and with the generous permission of officials of the Geological Survey of Canada, the silicified material described in the following pages was also sent to me. I regard it as belonging to a species of *Hemiarges* distinct from that found by Mr. Ormiston. According to Tripp (1958, p. 577) the only Silurian species of *Hemiarges* known from North America is one described by Hall and Clarke from New York State. The original material is redescribed here, and is a species not unlike those from Cornwallis Island. Some affinity is thus suggested between the Arctic and New York State Upper Silurian trilobites. Relationships between the Arctic Silurian shelly faunas and those farther south in North America are not particularly evident from the studies reported on by Thorsteinsson (1958, p. 70–74).

I am indebted to the gentlemen mentioned for encouraging me to study this material, and to Mr. Clinton F. Kilfoyle for the loan of type material from the New York State Museum (NYSM). The initials GSC precede catalogue numbers of the Geological

[1] A portion of the cost of the plates in this paper was borne by the author.

Survey of Canada, MCZ those of the Museum of Comparative Zoology, Harvard University. Ronald P. Tripp has been most helpful in discussing the taxonomy of the *Hemiarges* group, and in lending me photographs of various British species. Miss Susan Fenollosa made the enlargements from my negatives and aided in preparing the plates.

MORPHOLOGY AND TERMINOLOGY

Terminology applicable to lichids was discussed by Tripp (1957, p. 105, text-fig. 1) and Harrington, Moore & Stubblefield (*in* Moore, 1959, p. O117–O126). Here the term glabella is used to include the occipital ring. In lichids the glabella in front of the occipital ring is divided by longitudinal furrows, which run back from the inner end of lateral glabellar furrow 3p, into a median lobe (or central area) and lateral lobes. In the species of *Hemiarges* discussed below two large lateral lobes are evident, separated by a deep, outward and slightly forwardly directed lateral glabellar furrow, 1p. The lobe in front of this furrow is the bicomposite lobe, formed by the fusion of lateral glabellar lobes 2p and 3p. In *H. ormistoni*, n. sp. (pl. 57, fig. 29), there is an indentation in the longitudinal furrow at about the mid-length of the bicomposite lobe, and this indentation probably indicates the position of the inner end of lateral glabellar furrow 2p. The lobe behind lateral glabellar furrow 1p is here called the posterior (or basal) lateral glabellar lobe (pl. 55, figs. 1,12; pl. 56, fig. 23), is subcircular in outline and convex. The axial furrow between this lobe and the eye lobe is shallow, and posterolaterally its course presumably follows the sharp change in slope between the lobe and the fixed cheek. There is no indication of an occipital lobe, so presumably in these species this lobe is completely fused with the basal lateral lobe. That part of the median glabellar lobe lying between the basal lateral lobes is relatively depressed, particularly along a transverse line which lies just behind the junction of the longitudinal and lateral furrows 1p. In *H. aquilonius* n. sp. (pl. 56, figs. 23,26) this depression is marked, and gives the appearance that "the posterior lateral furrows are connected across the median lobe of the glabella" (Tripp, 1957, p. 117).

SYSTEMATIC PALAEONTOLOGY

Family LICHIDAE Hawle & Corda, 1847
Subfamily CERATARGINAE Tripp, 1957
Genus HEMIARGES Gürich, 1901

Discussion.—Tripp (1957; 1958; 1959, *in* Moore, p. O495–O504) has recently given a new classification of this family and discussed both the stratigraphical and geographical distribution of the species and their evolution. He conceived of the genera broadly, and placed *Richterarges* and *Choneilobarges* of Phleger, 1936, in the synonymy of *Hemiarges*. The type species of *Hemiarges* is *H. wesenbergensis* (Schmidt, 1885, p. 44–46, pl. 6, figs. 1,2,4?; Öpik, 1937, p. 63–64, pl. 22, fig. 7, text-fig. 18; Tripp, 1957, text-fig. 5J, left side), from the Upper Ordovician of Estonia. In this species only the inner part of lateral glabellar furrow 1p is present, so that the bicomposite lobe is partially confluent with lateral lobe 1p, the longitudinal furrows form a curve that is moderately convex inwards so that the median glabellar lobe is narrowest at about the mid-length, the occipital lobes are partially defined, and the eye lobe is situated well out on the cheek, the mid-point in advance of lateral glabellar furrow 1p. This species, and others like it from the Ordovician and Silurian of Europe and North America, are thus different from those described here. In these specimens (pl. 55, figs. 1,12; pl. 56, figs. 23,26) lateral glabellar furrow 1p is complete, the longitudinal furrows tend toward being straight and subparallel, the posterior part of the median lobe is depressed, the occipital lobe is not defined, and the palpebral lobe is situated adjacent to the axial furrow, the midpoint in line with or behind the inner end of lateral glabellar furrow 1p. These species appear to belong to the group which "differs from typical species of *Hemiarges* in that the bicomposite lobes are usually circumscribed," i.e. lateral furrow 1p is complete, "and the posterior lateral furrows are often connected across the median lobe of the glabella" (Tripp, 1957, p. 117). Tripp places in this group *H. maccullochi* (Reed, 1914, p. 28–29, pl. 4, figs. 9,10) from the Upper Ordovician of Scotland, and another member may be the British Middle Silurian species *H. bucklandi* (Tripp, 1957, text-fig.

3A; 1958, p. 580–581, pl. 85, figs. 13–16). As Tripp remarked, in this group there is much variation in the features of the glabella by which he characterized it. If other features—position of eye lobe, outline of anterior cephalic margin, characters of pygidium, for example—are taken into account, it becomes evident that not only are they differently developed in different species, but combined in a multiplicity of ways. A workable diagnosis separating this group from "typical" *Hemiarges* becomes impossible to frame. I have therefore followed Tripp's broad concept of *Hemiarges*.

The absence of spines on the border of larger pygidia is a feature that *Hemiarges ormistoni* n. sp. (pl. 55, figs. 19–21) shares with *H. heteroclytus* (Barrande, 1846; see Horný, Prantl, & Vaněk, 1958, pl. 8, figs. 5,6), and *H. maia* (Reed, 1921, p. 222, 1 text-fig.). The cranidium of *H. heteroclytus* is of the *H. wesenbergensis* type, that of *H. maia* not described.

Tripp (1957, p. 117) remarked that *H. ptyonurus* and species like it approached *Acanthopyge* in glabellar lobation. Comparison of the present silicified material of *H. aquilonius*, n. sp., with similar material of *Acanthopyge* (Whittington, 1956, pl. 131, figs. 7–11,13,20) shows the truth of this statement. The glabella of *A. consanguinea* is far more convex longitudinally than that of *H. aquilonius*, and the depression of the posterior part of the median glabellar lobe more marked. The position of the eye lobe is similar in the two species. Distinctive of *Acanthopyge* is the forward position of the librigenal spine, and the deep notch in the border behind it, as well as the type of pygidium. It seems likely, as Tripp indicates (1957, text-fig. 7) that *Acanthopyge* is derived from *Hemiarges*, perhaps from species of the type described here.

HEMIARGES PTYONURUS
(Hall & Clarke, 1888)
Pl. 55, figs. 1–9,11

Lectotype (here selected).—NYSM 4555, cranidium, original of Hall and Clarke, 1888, plate 19B, figure 19, preserved in a brown siltstone, Upper Silurian, Cobleskill limestone, Schoharie, Schoharie County, New York.

Other material.—NYSM 4556, pygidium; NYSM 4557, incomplete pygidium, immediately in front of which is a thoracic segment and in front of that a free cheek exposed from the ventral side. The two specimens are the originals of Hall and Clarke, 1888, plate 19B, figures 20 and 21 respectively, preserved in the same type of rock as the lectotype and from the same horizon and locality.

Description.—Cranidium of length (sag.) 5.9 mms. Glabella narrowest across the moderately convex occipital ring, which is of width (tr.) 3.5 mms., the posterior margin straight, the anterior margin curved forward so that the ring is shortest distally. In front of occipital ring glabella widens rapidly to a maximum width of 6.5 mms. immediately behind the palpebral lobes, in front of here glabella narrows gradually forward to rounded margin of anterior lobe. Glabella is flattened medially, distal slopes moderate, the median part of the glabella extending no higher than the palpebral lobes. Longitudinal furrow is evident at about one-quarter the length from the anterior margin, and deepens posteriorly to a maximum at the junction with lateral glabellar furrow 1p; behind this point longitudinal furrow broad and shallow but extending back to occipital ring; the longitudinal furrows isolate a subparallel-sided median glabellar lobe which is only slightly narrower (tr.) than the bicomposite lobe. Latter not defined anteriorly by lateral glabellar furrow 3p, defined on the proximal side by the longitudinal furrow, posteriorly by the deep, straight, broad, forward- and outwardly-directed lateral glabellar furrow 1p, and displaying a slight independent convexity. The posterior lateral glabellar lobe is separated only by the axial furrow from the palpebral lobe, posterolaterally the curving margin runs from behind the palpebral lobe to the outer end of the occipital furrow; the lobe is moderately convex, the steepest slope being the posterior. Between the posterior lateral lobes the median glabellar lobe is gently conxex, and may be described as depressed since it lies at a slightly lower level than the inner, highest parts of the posterior lobes (pl. 55, figs. 2,3). Axial furrow shallow and broad, behind the palpebral lobe its course indicated rather by the sharp change of slope between posterior

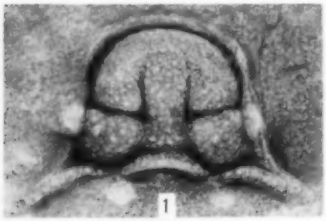
lateral lobe and fixed cheek than by a furrow. Anterior pit barely visible but probably represented by the deepest part of the axial furrow at the anterolateral corner of the glabella. Preglabellar furrow shallow, anterior border narrow (sag. and exs.), gently convex. Palpebral lobe relatively short, semicircular in outline, horizontal, surface about level with highest part of posterior lateral lobe. Anterior branch of suture runs straight forward and slightly inward parallel to the axial furrow and separated from it by a narrow strip of fixed cheek, then curves inward across anterior border of cephalon to join rostral suture. Posterior branch of suture runs backward and slightly outward, distally curving more strongly outward as it crosses the posterior border furrow and posterior border at an oblique angle. Posterior part of fixed cheek is thus triangular, broad (tr.), consisting mostly of the convex posterior border which curves outward and gently backward, but including the small depressed region between the posterior border furrow, the posterior lateral glabellar lobe and the posterior branch of the suture. External surface bearing close-spaced tubercles, which are largest on the posterior half of the glabella and the posterior border, symmetrical paired arrangement of tubercles not evident.

Pygidium subtriangular in outline (NYSM 4557 of length (sag.) 8.5 mms., maximum width 11 mms.). Axis gently convex, tapering slightly back and extending beyond half the length, continued to posterior margin by a relatively broad (tr.), gently convex postaxial ridge; length of axis about 1½ times that of postaxial ridge. First two rings of axis defined by deep ring furrows which curve backward distally, the anterior slope of each furrow being much the steepest, so that the first ring stands above the second and the second above the remainder of the axis (pl. 55, fig. 9). Some seven additional axial rings are indicated by extremely faint ring furrows or by paired tubercles. Axial furrows broad and deep. Inner part of pleural regions horizontal, gently convex, outer part bent to slope down moderately steeply to broad shallow border furrow. Border of pygidium of about equal width to border furrow and to posterior bands of first two pleurae, moderately convex. First and second pleurae well defined by posterior pleural bands, band of anterior pleura runs transversely outward from first ring, at about half the width of the pleural region curving back and after crossing the border continuing as a backwardly directed marginal spine. The posterior band is an evenly convex ridge of about the same width (exs.)

Explanation of Plate 55

Figs. *1–9,11—Hemiarges ptyonurus* (Hall & Clarke, 1888), Cobleskill limestone, Upper Silurian, Schoharie, Schoharie County, New York. *1–4*, lectotype, cranidium, NYSM 4555, original of Hall and Clarke, 1888, pl. 19B, fig. 19, dorsal, anterior, right lateral, oblique views, ×4. *5–7*, pygidium, NYSM 4557, original of Hall & Clarke, 1888, pl. 19B, fig. 21, dorsal, posterior, right lateral views, ×3. *8,9,11*, pygidium, in front of which is detached thoracic segment and free cheek, NYSM 4556, original of Hall & Clarke, 1888, pl. 19B, fig. 20, posterior, left lateral views of pygidium, dorsal view of pygidium, posterior view of segment and interior view of free cheek, ×3.

10,12–21—Hemiarges ormistoni, n.sp., upper part of Cape Phillips formation, Cape Phillips, Cornwallis Island, Northwest Territories, Canada. *10,14*, hypostome, MCZ 5624 B, right lateral and exterior views, ×6. *12,13,15,18*, holotype, MCZ 5623, incomplete cranidium, dorsal, right lateral, anterior, oblique views, ×4. *16*, pygidium, MCZ 5624 C, dorsal view, ×3. *17*, pygidium, MCZ 5624 D, dorsal view, ×6. *19–21*, pygidium, MCZ 5624 A, dorsal, left lateral, posterior views, ×2.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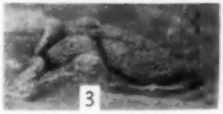
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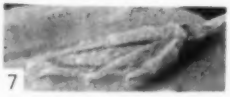
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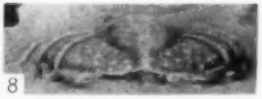
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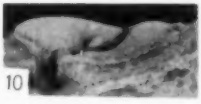
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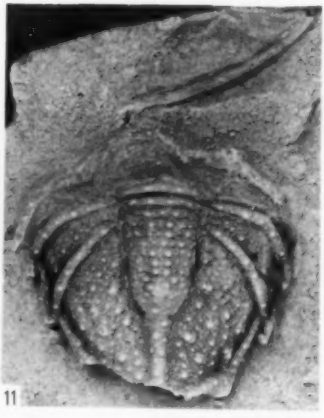
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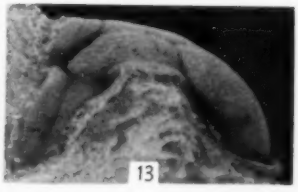
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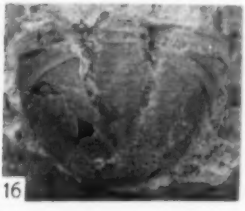
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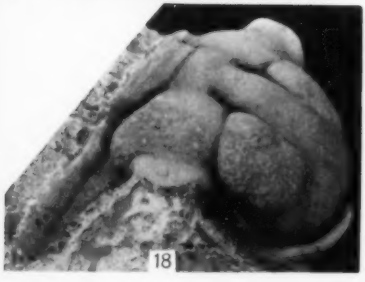
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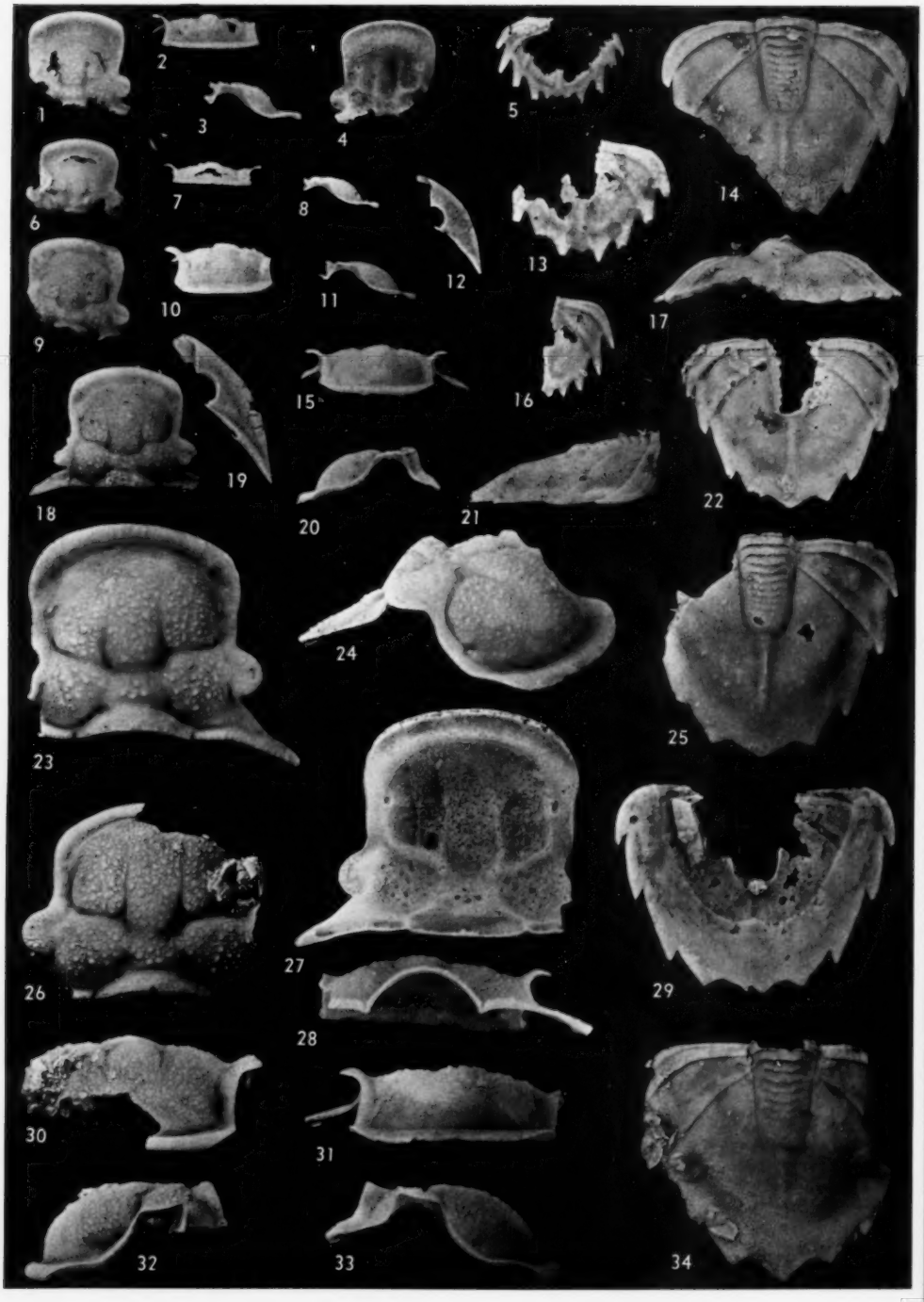
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as the axial ring, the anterior pleural band flattened and widening distally. Second pleura with posterior pleural band running outward and backward from second axial ring, curving distally and crossing border to be continued as a posteriorly directed marginal spine. Anterior band much wider (exs.) than posterior, flat. At about midway along the border of the pygidium between the second marginal spine and the midline is a third marginal spine, and close to the midline is a fourth marginal spine, both these spines being backwardly directed and of about the same thickness as the first and second. External surface bearing close spaced small tubercles and more widely scattered larger tubercles; these larger tubercles are arranged in rows along the axial rings, in most rings there being a symmetrical pair situated closer to the midline in successively posterior rings. On the pleural regions large tubercles are spaced along the two prominent posterior pleural bands and scattered on the pleural region and postaxial ridge inside the border furrow.

Discussion.—Hall & Clarke (1888, p. 87, pl. 19B, fig. 20) describe a single detached thoracic segment, that lying in front of the pygidium NYSM 4556, only the edge of which is exposed (pl. 55, fig. 11). It may belong to this species. Immediately in front of this thoracic segment is a free cheek (pl. 55, fig. 11), exposed from the ventral side, and this may be that referred to by Hall & Clarke (1888, p. 87). The broad-based librigenal spine is typical of *Hemiarges*, as is the outline and width of the borders (compare pl. 57, figs. 22–24). Close to the anterior branch of the suture the lateral border curves more strongly forward. The outline of the anterolateral margin of the cephalon is therefore angulate, as it is in, for example, *H. bucklandi* (Tripp, 1957, text-fig. 3A).

The cranidium of *H. ptyonurus* is like that of both the species from Cornwallis Island, but may be distinguished from that of *H. aquilonius* in that the median part of the glabella, particularly in front of the level of lateral glabellar furrows 1p, is flattened rather than reaching a maximum height at the midline, in that the palpebral lobes are shorter (exs.), and in that the anterior branches of the facial suture converge slightly forward. The tuberculation on the external surface of *H. ptyonurus* is like that in *H. aquilonius*, though appearing coarser and more prominent on the posterior border of the cranidium. From the cranidium of *H. ormistoni* that of *H. ptyonurus* is distinguished by the lesser inflation of the glabella in front of the occipital ring, the absence of lateral glabellar furrow 3p, the shorter (exs.)

EXPLANATION OF PLATE 56

FIGS. *1–34*—*Hemiarges aquilonius*, n. sp., Read Bay formation (member C), locality 21, near Cape Hotham, Cornwallis Island, Northwest Territories, Canada. *1–4*, incomplete small cranidium, GSC 15247, dorsal, anterior, right lateral, ventral views, ×8. *5*, incomplete transitory pygidium, GSC 15251, dorsal view, ×6. *6–8*, incomplete small cranidium, GSC 15248, dorsal, anterior, right lateral views, ×6. *9–11*, incomplete small cranidium, GSC 15249, dorsal, anterior, right lateral views, ×6. *12*, small free cheek, GSC 15248, dorsal view, ×6. *13*, incomplete pygidium, GSC 15252, dorsal view, ×6. *14,17,21*, paratype pygidium, GSC 15245, dorsal, posterior, right lateral views, ×3. *15,18,20*, cranidium, GSC 15250, anterior, dorsal, left lateral views, ×6. *16*, incomplete pygidium, GSC 15253, dorsal view, ×4. *19*, free cheek, GSC 15250, dorsal view, ×6. *22*, incomplete pygidium, GSC 15259, dorsal view, ×4. *23,24,27,28,31,33*, holotype cranidium, GSC 15242, dorsal, oblique, ventral, posterior, anterior, right lateral views, ×4½. *25*, incomplete pygidium, GSC 15255, dorsal view, ×3. *26,30,32*, incomplete cranidium, GSC 15258, dorsal, anterior, left lateral views, ×3. *29*, incomplete pygidium, GSC 15256, ventral view showing doublure, ×3. *34*, incomplete pygidium, GSC 15257, dorsal view, ×3.

palpebral lobe, and the presence of prominent tuberculation on the external surface.

The pygidium of *H. ptyonurus* is distinguished from that of *H. ormistoni* by the relatively longer axis and broader (tr.) postaxial ridge, the more prominent posterior bands of the first and second pleurae, the presence of marginal spines and the tubercles on the external surface. It is more like that of *H. aquilonius* but again the axis is relatively longer and the postaxial ridge broader, and further, the posterior pleural bands of the first two pleurae are convex and have a similar slope on either side, not a much steeper posterior slope, there is a border, and no median posterior spine on the margin. The external surface is granulate, and bears more numerous and larger tubercles.

HEMIARGES ORMISTONI n. sp.
Pl. 55, figs. 10, 12–21; pl. 57, fig. 29

Holotype.—MCZ 5623, incomplete cranidium, from gray argillaceous limestone of the Cape Phillips formation, Cape Phillips, close to the coast and south of the creek at the southern end of Thorsteinsson's locality 19 (1958, map 1054 A), Cornwallis Island, Northwest Territories, Canada. Collected by Allen R. Ormiston, June, 1959. The rock also contains abundant brachiopods, kindly identified by Professor Arthur J. Boucot as *Atrypella* cf. *scheii* (Holtedahl). This brachiopod has been recorded by Thorsteinsson (1958, p. 74) from many horizons in the Read Bay formation, and also in the Middle Ludlovian portion of the Cape Phillips formation (1958, p. 103). Judging from the locality from which the trilobite came, and the dip and strike of the rocks at Thorsteinsson's locality 19, it appears likely that the horizon is in the upper part of the Cape Phillips formation, i.e. in the Middle Ludlovian.

Other material.—MCZ 5624, the specimens figured here and in addition three incomplete cranidia, a hypostome, and three pygidia; all from the same locality and horizon.

Description.—The holotype cranidium (pl. 55, figs. 12,13,15,18; Pl. 3, fig. 29) differs from one of a similar size of *H. aquilonius* (pl. 56, figs. 26,30,32) in that the glabella appears more inflated and consequently stands up higher. The basal lateral lobe slopes gently outward to the gentle change of slope at the axial furrow; the longitudinal furrow is deepened at, and a short distance behind, its junction with lateral glabellar furrow 1p, elsewhere it is extremely shallow or virtually absent. The bicomposite lobe has a gentle independent convexity so that a change of slope defines its anterior as well as inner margin, and a slight indentation in the longitudinal furrow at about half the length of this lobe suggests the position of the proximal part of lateral glabellar furrow 2p. The outermost part of the anterior lobe in front of the bicomposite lobe (pl. 55, figs. 13,15,18) also displays a gentle independent convexity suggestive of lateral glabellar lobe 4p. The occipital ring appears to be more convex than that of *H. aquilonius*, for the posterior part of the median glabellar lobe is not at all depressed below the adjacent part of the posterior lateral lobe, and is separated from the occipital ring by only a faint occipital furrow; distally the occipital ring narrows, the occipital furrow deepens, and the posterior lateral lobe slopes steeply back. These remarks apply to the external surfaces of the exoskeletons—in internal moulds the median part of the occipital furrow and lateral glabellar furrow 1p appear much broader and deeper, and the posterior part of the median lobe depressed. The anterior border of the cranidium in *H. ormistoni* is relatively narrower (sag. and exs.) and more convex.

The hypostome differs from that of *H. aquilonius* (compare pl. 55, figs. 10,14 with pl. 57, figs. 6,15) in details of outline, convexity, and relative size of different parts—for example, the lateral margins of the middle body converge less strongly backward, the anterior lobe of the middle body is more inflated distally and the anterior wing more sharply bent upward. The posterior lobe of the middle body is relatively longer medially, and the posterior border relatively wider (sag. and exs.), with a deeper and better defined median notch and a greater convexity medially. There is a narrow (sag. and exs.) anterior border, best-defined distally; such a border is absent in larger cephala of *H. aquilonius*.

The largest pygidia (pl. 55, figs. 19–21) differ most obviously from those of *H.*

aquilonius (pl. 56, figs. 14,17,21,25,34) in the greater convexity of the pleural regions, which lack the concave flattening distally, and in the absence of marginal spines. The only indication of such spines is a slight angulation in the posterolateral margin which might indicate the position of the fourth pleural spines. The interpleural furrows run in a gentle curve but are less strongly backwardly directed. The smallest pygidium available of *H. ormistoni* (pl. 55, fig. 17, 5 mms. in length) shows the presence of four pairs of marginal projections and a median posterior projection. The first and second of these are situated at the ends of the first and second posterior pleural bands and are extremely short and blunt. The third and fourth are slight, blunt projections of the scalloped posterolateral margin, and the posterior median projection is similar. In pygidia intermediate in size the first and second spines are absent, the third and fourth being merely low and rounded projections where there is a slight change in the direction of the margin.

External surface of cranidium (pl. 57, fig. 29) and pygidium impressed, except in the furrows, by small, shallow close-spaced pits. This pitting seems to affect the entire thickness of the exoskeleton, for the same pattern is visible on internal moulds. On the bicomposite and posterior lateral lobes of the glabella there is also a low granulation, these granules being largest and most conspicuous on the posterolateral slope of the posterior lobe. On the anterior border of the cranidium there are anastomosing terrace lines running subparallel to the margin. On the outer parts of the pleural region of the pygidium granules, of a similar diameter and density to the pits, are present and become especially conspicuous on the posterolateral margins. The external surface of the middle body of the hypostome (pl. 55, fig. 14) and the posterior border are not pitted, on the lateral borders there are prominent anastomosing terrace lines running subparallel to the margin, which die out posteriorly.

Discussion.—Only two other species of *Hemiarges*, having a pygidium of length (sag.) 12 mms. or more which lacks marginal spines, are known. One is *H. heteroclytus* (Barrande, 1846, p. 47; 1852, p. 608, pl. 28, figs. 33,34; Horný, Prantl, & Vaněk, 1958, pl. 8, fig. 5) from the Upper Silurian of Bohemia. While the outline and general form is not unlike that of *H. ormistoni*, *H. heteroclytus* has a relatively longer axis and the outer parts of the pleural regions are concave. The second species is *H. maia* (Reed, 1921, p. 219–220, fig.) from the Middle Silurian of England. This is a relatively shorter and broader pygidium than that of *H. ormistoni* and also has a relatively longer axis. Thus neither of these European pygidia appears to be much like that from Cornwallis Island, and the cranidium of *H. heteroclytus* (Horný, Prantl & Vaněk, 1958, pl. 8, fig. 6) is not like that of *H. ormistoni* (the cranidium of *H. maia* is not known).

HEMIARGES AQUILONIUS, n. sp.
Pl. 56, figs. 1–34; pl. 57, figs. 1–28

Holotype.—GSC 15242, incomplete silicified cranidium, from Read Bay formation, approximately 500 feet above base of member C, Middle Ludlovian, locality 21, near Cape Hotham (Thorsteinsson, 1958, p. 68, this locality being erroneously marked as number 26 on map 1054A), Cornwallis Island, Northwest Territories, Canada.

Other material.—Paratypes GSC 15243–15246; figured specimens GSC 15247–15265, and many additional parts of exoskeletons from same locality and horizon. In addition to the stromatoporoid, rugose and tabulate corals listed by Thorsteinsson (1958, p. 68) the silicified blocks prepared by Whittington contained not only abundant parts of the single trilobite species but sponge spicules, one or two brachiopods, and crinoid columnals.

Description.—Largest cranidium known of length about 12.0 mm. (pl. 56, figs. 26,30,32), maximum width of cephalon about twice the length, moderately convex. Glabella narrowest (tr.) across occipital ring, in front of ring expanding rapidly to maximum width which is in line with most posterior part of eye lobe; in front of maximum width straight-sided, tapering gradually to rounded anterolateral margin, anterior margin gently curved. Posterior margin of occipital ring straight, anterior margin defined by the occipital furrow which curves convexly forward so that the ring is longest sagitally and narrow (exs.) distally. Occipital furrow deepened behind posterior

lateral glabellar lobe. Lateral glabellar furrow 3p extremely faintly defined on external surface (pl. 56, fig. 24), better seen as low ridge on internal surface (pl. 56, fig. 27); furrow 3p commences at axial furrow beside anterior pit and diverges forward and inward from this furrow, curving around through almost 180° to be continued directly back as the longitudinal furrow. This latter furrow deepens back to a maximum at the junction with lateral glabellar furrow 1p. At this junction, which is in line with the anterior part of the eye lobe, is a deep three-pointed depression. The anterior of these points merges into the longitudinal furrow, the lateral point is directed forward and outward into lateral glabellar furrow 1p, the posterior point is directed backward and inward and continued directly back by a shallow depression that bounds the inner side of the posterior lateral lobe, and by a shallow depression that crosses the median glabellar lobe. The glabella is thus subdivided into a straight-sided median lobe which is of about the same width as the bicomposite lobe and which merges forward into the short (sag. and exs.) but wide anterior lobe. The posterior part of the median lobe, lying between the posterior lateral lobes, is depressed. The bicomposite lobe is longer than wide, defined distally by a shallow axial furrow and posteriorly by the relatively broad, deep, diagonally-directed lateral glabellar furrow 1p. The posterior lateral glabellar lobe is subcircular in outline, the diameter greater than the maximum width of the bicomposite lobe; on the distal side it is bounded by an extremely shallow axial furrow between it and the fixed cheek in front of the palpebral lobe, by the change in slope between it and the palpebral lobe, and by a sharp change in slope between it and the fixed cheek behind the palpebral lobe. Proximally the posterior lateral lobe is bounded by lateral glabellar furrow 1p, by the broad, shallow longitudinal furrow, and the distal and deeper part of the occipital furrow. Ceratarginae are characterized by Tripp (1957, p. 117) as having the "axial furrows usually obsolete behind bicomposite lobes," that is, the axial furrow is difficult to discern as a furrow beside the posterior lateral glabellar lobe. In the present species there is no difficulty in tracing the distal boundary of this posterior lateral lobe but it is defined rather by a change in slope than by a distinct furrow. Axial furrow beside bicomposite lobe shallow, continuous with shallow preglabellar furrow. Deep anterior pit with a rounded tubercle situated on the anterior slope of the pit (pl. 56, figs. 23,24), on the inner surface (pl. 56, fig. 27) the anterior boss bears a corresponding depression on its anterior slope. Cheek having large eye lobe situated on highest part, which is inner posterior corner, mid-point of eye lobe in line with anterior edge of depressed part of median glabellar lobe. Outside eye lobe cheek slopes at first steeply, then more gradually, passing distally into a concave portion which in turn merges into the broad, gently convex border; lateral and anterolateral border continued on cranidium as anterior border which is separated from the glabella only by the preglabellar furrow. Posterior border of cheek narrow (exs.) and convex adjacent to axial furrow, broadening distally and becoming of the same width as the lateral border, posterior border furrow shallow. Posterolaterally cheek drawn out into triangular genal spine, the median part of which is depressed between the convex continuations of the borders. Margin of cephalon rolled under to form the broad doublure which, inside the border, lies close against the dorsal exoskeleton; anteriorly inner margin of doublure lies beneath most anterior part of glabella, laterally and posterolaterally doublure extends in to margin of eye lobe and beneath genal spine (pl. 57, figs. 12,22), posteriorly doublure narrows rapidly and does not extend beneath inner part of posterior border (pl. 56, fig. 27). Palpebral lobe with extremely faintly defined, gently convex rim, shallow median depression. Eye surface convex, bounded at lower margin by a shallow furrow. Anterior branch of facial suture runs directly forward parallel to the axial furrow until it reaches the anterior border, where it curves around on to the vertical outer margin (pl. 57, fig. 1). Here it meets the rostral suture and this suture runs along the vertical outer slope of the anterior border of the cranidium (pl. 56, fig. 27; pl. 57, fig. 11). Connective suture runs first inward and backward, then, beneath about the mid-point of the border, it curves abruptly through 90° and runs out-

ward and backward to the inner margin of the doublure. The rostral plate (pl. 57, figs. 11,12,17) is thus wider (tr.) than long, the lateral margin indented, and the posterolateral corner forms a long slim projection. Posterior branch of suture runs straight backward and strongly outward from the eye lobe to curve across the posterior border inside the base of the librigenal spine.

The straight portion of the anterior margin of the hypostome (pl. 57, figs. 6,10,11–15,17) is the sutural margin, which fitted against the straight posterior edge of the rostral plate between the projecting points. Middle body sub-lozenge shape, middle furrows short, deep and transverse, isolating a wide (tr.) but short posterior lobe of the middle body, the distal parts of which are inflated. Just behind greatest width of middle body the lateral edge of the exoskeleton is curved upward and extended dorsally as a blunt anterior wing. Lateral border with sharp shoulder, posterior border broader than lateral and having a wide, shallow notch in the posterior margin. Doublure extends beneath lateral and posterior borders, the posterior edge in the middle part of the notch folded abruptly to form a sharper edge than is developed posterolaterally. Inner edge of doublure is curved dorsally, the median part of the edge folded back again to form a projecting lip (pl. 57, figs. 18,19). On the posterior, vertical, side of this lip there is a median ridge flanked by a pair of lower, blunter ridges, and running back across the doublure in the sagittal line is a groove flanked by low ridges. Beneath lateral border inner edge of doublure is not folded over and in most specimens is broken, so that whether or not a posterior wing is developed cannot be determined.

Thorax of at least nine segments (pl. 57 fig. 21). Isolated fragments of segments (pl. 57, figs. 25–28) show the narrow (sag. and exs.), flat axial ring, and the narrow, deep articulating furrow. At the anterior margin, below the axial furrow, is an articulating socket, and on the posterior margin a corresponding articulating boss. Pleurae broad (tr.) and short (exs.), the outer part flexed gently down and about one and one-half times as wide as the flat inner part, broader and blade like, the tip curving back. Doublure extends inward for about two-thirds the width of the outer part, shallow panderian notch in the inner margin. Pleural furrow narrow, becoming deeper toward the fulcrum, deepest outside here and dying out at the inner edge of the facet. Pygidium subtriangular in outline, gently convex, axis tapering gradually back and extending to about half the length (sag.), continued to margin by a low, narrow postaxial ridge. Axis subdivided by about 11 ring furrows, the first two of these furrows curving back distally (the second furrow more strongly than the first), and reaching the axial furrow. Behind the mid-part of the first and second rings the ring furrow is deeply excavated, sloping downward and inward, so that the posterior edge of these rings is well defined and projects backward from the axis. Succeeding ring furrows do not extend to the axial furrows, and are successively less deeply impressed. Pleural regions horizontal adjacent to axis, distally curving down to flattened outer parts. First and second interpleural furrows strongly marked, the anterior slope overhanging so that the edge of the pleura is well defined and backwardly projecting; these interpleural furrows curve outward and backward and the distal part of the pleura is extended as a backwardly directed blade-like spine. First pleura having the pleural furrow situated closer to the anterior than the posterior margin, shallow and running out to the base of the pleural spine. Pleural furrow faintly defined on second pleura, closer to posterior than anterior margin. Behind second pleurae margins of pleural regions bear two pairs and a median spine, these spines successively blunter, the posterior median spine being obliquely pointed. Doublure broad, close to dorsal exoskeleton, extending in beneath the flattened outer parts of the pleural regions to about half the width, in midline a blunt projection on inner margin.

External surface of glabella, palpebral rim and posterior border tuberculate, tubercles low, rounded, varying in size and closely and irregularly spaced. Only some of the largest (such as that in the center of the posterior lateral lobe) suggest a symmetrical paired arrangement. Cheek and lateral and anterior borders of cephalon apparently smooth. Small, close-spaced tubercles along posterior margins of axial rings and pleurae. More

widely spaced larger tubercles occur also on these margins (except axial rings of thorax), and are irregularly placed except on the axial rings of the pygidium, where they are roughly paired. On larger pygidia scattered tubercles may be seen on the pleural regions behind the second interpleural furrow, and in some specimens one or two such tubercles and an extremely faint ridge outline the ridge immediately in front of the third interpleural furrow. The silicification of the exoskeletons in this material is of a type that shows concentric beekite rings, and apparently does not preserve the finest details—one or two specimens suggest that between the larger tubercles and on the apparently smooth distal parts of the exoskeleton there may be the characteristic granulation of the lichids.

Development.—The smallest cranidium is of length (sag.) about 2.2 mms. (pl. 56, figs. 1–4). The highest part of the glabella is the median lobe, which stands only slightly below the level of the palpebral lobes; lateral lobes of glabella much less inflated than in larger specimens, the bicomposite lobe not outlined anteriorly, the posterior lateral lobe lying below the level of the posterior part of the median glabellar lobe. Anterior lobe of glabella gently sloping, vaguely outlined and separated by a broad (sag. and exs.) concave region from the anterior border. Anterior branches of facial suture diverge forward, relatively broad part of fixed cheek enclosed between these sutures and the glabella. As the size of the cranidium increases (pl. 56, figs. 6–11,15,18, 20) the glabella increases in convexity particularly by inflation of the bicomposite and posterior lateral lobes. Thus in largest cranidium (pl. 56, figs. 26,30,32) the median part of the glabella stands as high as the palpebral lobe, and the longitudinal profile slopes steeply forward, approaching the vertical at the preglabellar furrow; this expansion of the glabella seems to take place at the expense of the area in front of it, so that in the largest cranidium the anterior lobe is separated only by a relatively narrow preglabellar furrow from the anterior border. As the inflation of the bicomposite lobe proceeds it becomes better defined anteriorly and laterally; the inflation of the posterior lateral lobe results in its standing higher than the posterior part of the median lobe in larger cranidia, thus the latter becomes depressed relative to the surrounding parts of the glabella. The increase in convexity of the glabella does not seem to affect greatly the occipital ring, so that the slope down to this ring from the posterior lateral lobe becomes notably more steep. The smallest hypostome known (pl. 57, figs. 4,5) belongs with a cranidium of about the size of the original of pl. 56, figs. 6–8. In the small hypostomes there is a faintly defined border to the middle body anterolaterally, and the posterior lobe of the middle body is relatively larger. Apparently as the anterior part of the glabella expands forward and upward with increasing size, so the anterior lobe of the middle body of the hypostome expands relatively outward and backward. In the largest specimens (pl. 57, fig. 6) it is seen to lie close against the border beside the shoulder and the posterior lobe is relatively restricted. In the smaller hypostomes the ridges and grooves on the postero-median part of the doublure are present but relatively less strongly developed.

The smallest pygidium (pl. 56, fig. 5) is incomplete, approximately 2 mms. in length (sag.). On the lateral margins there are 4 pairs of long slim spines, and on the posterior margin may be seen the broken bases of a fifth pair and a median spine. On the outer parts of the pleural regions posterior bands of the first three pleurae, corresponding with the first three pairs of border spines, may be distinguished. Thus this pygidium appears to include an additional segment to that in larger pygidia, and may be a late meraspid transitory pygidium. Larger pygidia (pl. 56, figs. 13,16) exhibit only four pairs and a median border spine, and the posterior bands of only the first two pleurae. These appear to be true pygidia but are distinguished from larger specimens (pl. 56, fig. 14) in that the border spines are relatively much longer. The transitory pygidium and the smallest true pygidia are relatively wider than larger pygidia.

Discussion.—In pl. 57, figs. 1,7,11,12,13, the various parts of the cephalon are shown in juxtaposition. The hypostome in these photographs is of a slightly larger size than belongs with the other parts of the cephalon. As in other trilobites, the sutural edges of

the exoskeleton are broad and flat, allowing a close fit along the lines of suture. Tripp (*in* Moore, 1959, fig. 393, 8b) gives an oblique ventral view of the cephalon of *Hemiarges scutalis* which has the rostral plate and hypostome in a similar position to that suggested here. A photograph of *Hemiarges bucklandi* (Milne Edwards, 1840) kindly sent to me by Mr. R. P. Tripp shows that this species from the Wenlock limestone of Britain has a rostral plate of similar shape to that of *H. aquilonius*.

Postscript: After the above was sent to the Editor, I received a copy of Vaněk, J., 1959, Čeled Lichaidae Hawle et Corda, 1847 ze středočeského staršího paleozoika (Trilobitae): Bohemia Centralis (A—Scientiae naturales), v. 1, fasc. 3, p. 77–168, pls. 1–12, 43 figs. (in Czech, brief English summary). A more extended description than any previously available of *Hemiarges heteroclytus* (p. 152–155, pl. 6, figs. 7–11, text-figs. 41–43) is given, based on isolated cranidia and pygidia, and an hypostome. The latter is like that of the American species described here. The cranidium is of *H. wesenbergensis* type, but lateral glabellar furrow 1p, is complete and deep.

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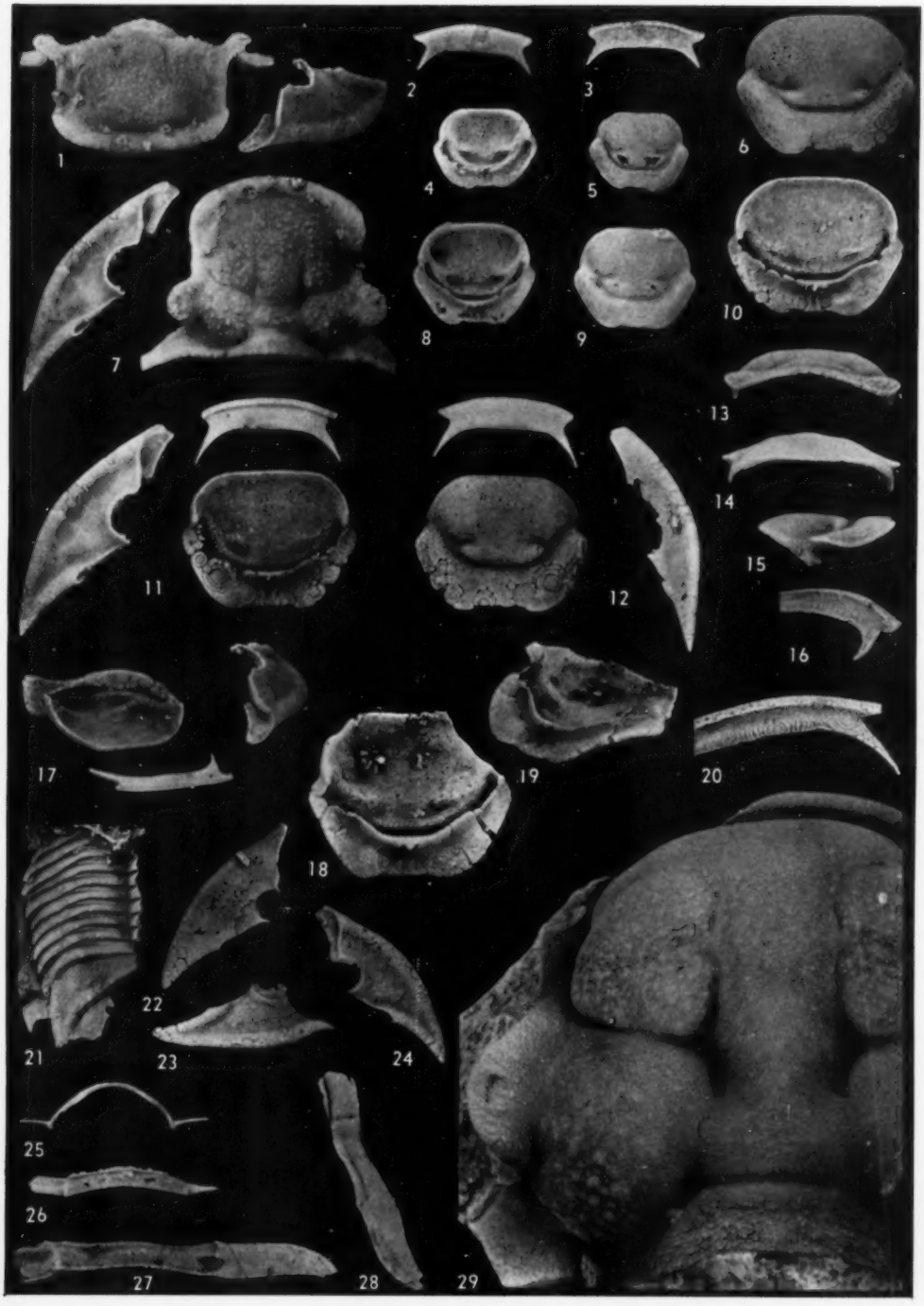
Manuscript received April 13, 1960

(*Explanation of Plate 57 will be found on page 444*)

Explanation of Plate 57

Figs. *1–28*—*Hemiarges aquilonius*, n. sp., Read Bay formation (member C), locality 21, near Cape Hotham, Cornwallis Island, Northwest Territories, Canada. *1,7*, cranidium and left free cheek, GSC 15260, anterior, dorsal views, ×6. *2,3*, small rostral plate, GSC 15263, exterior, interior views, ×9. *4,5*, small hypostome, (lost after photographing), interior, exterior views. ×9. *6, 10, 13–15*, paratype hypostome, GSC 15244, exterior, interior, posterior, anterior, right lateral views, ×4½. *8,9*, hypostome, GSC 15261, interior, exterior views, ×9. *11,12,17*, left free cheek, rostral plate, hypostome, GSC 15260, dorsal, ventral, oblique anterior views, ×6. *16,20*, part of large rostral plate, GSC 15262, oblique lateral, interior views, showing broad, flat, sutural edges, ×4½. *18,19*, incomplete hypostome, GSC 15254; two oblique interior views, showing posterior doublure with median ridges and grooves, ×6. *21*, part of nine thoracic segments and a pygidium, GSC 15265, dorsal view, ×3. *22–24*, paratype, right free cheek, GSC 15243, interior, lateral, exterior views, ×3. *25,26*, axial ring and inner part of pleurae of thoracic segment, GSC 15264, posterior, dorsal views, ×4½. *27,28*, paratype, part of axial ring and pleura of thoracic segment, GSC 15246, ventral view showing panderian notch in doublure, left lateral view, ×4½.

29—*Hemiarges ormistoni*, n. sp., holotype, incomplete cranidium, MCZ 5623, exterior view showing pitting and tuberculation of external surface, ×6.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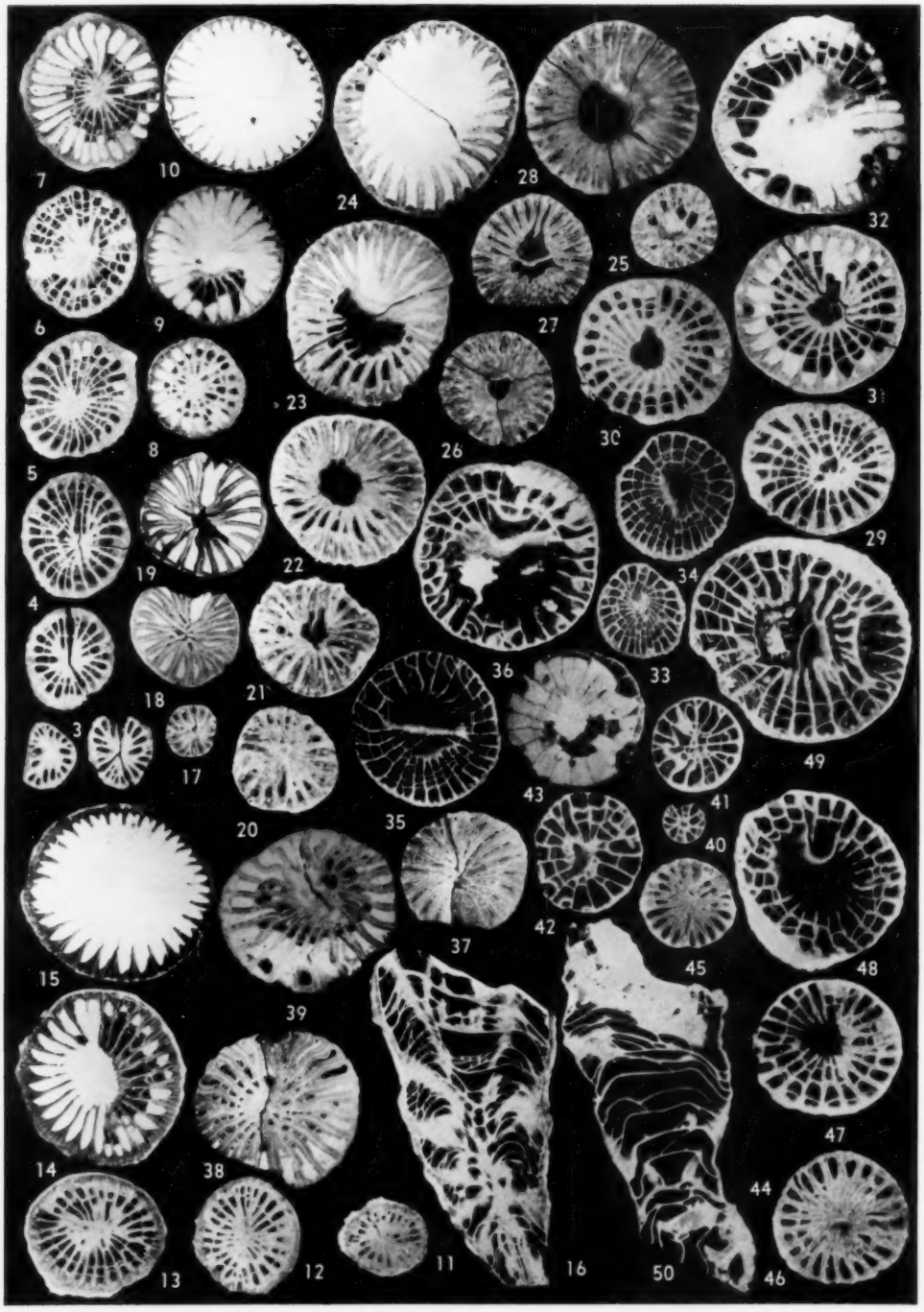
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THE METRIOPHYLLOID CORAL GENERA *STEREOLASMA*, *AMPLEXIPHYLLUM*, AND *STEWARTOPHYLLUM* FROM THE DEVONIAN HAMILTON GROUP OF NEW YORK

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ABSTRACT—Daniel Busch (1941, p. 392–411) described 6 new species of metriophylloid rugose corals from the Wanakah and Windom shales of the Hamilton group of western New York. After an examination of many serial sections of specimens from these beds it is suggested that Busch's species can be interpreted as growth stages or variants of the three common species *Stereolasma rectum* (Hall), *Amplexiphyllum hamiltoniae* (Hall), and *Stewartophyllum intermittens* (Hall).

INTRODUCTION AND ACKNOWLEDGMENTS

DANIEL BUSCH (1941) identified nine species of metriophylloid corals, six of them new, from two localities in the Wanakah shale and one locality in the Windom shale, both in the Middle Devonian Hamilton group of western New York. A large number of corals from these localities were obtained when the University of Michigan purchased the Raymond R. Hibbard collection of fossils from western New York. Sections were made of 150 metriophylloid corallites and serial sections were made of 25 of them.

Busch made a very detailed study of his corals but used variable structures in classifying his specimens. By using such features as corallite diameter, number of septa, nature of septa (amplexoid, dilation), character of fossilae, presence or absence of columella, number and nature of tabulae, and allowing for individual variation, the authors suggest that Busch's species can be interpreted as typical specimens or variants of the three common species *Stereolasma rectum* (Hall), *Amplexiphyllum hamiltoniae* (Hall), and *Stewartophyllum intermittens* (Hall).

The authors wish to thank Dr. Mildred Marple for the loan of Busch's types from the Ohio State University Geological Museum.

SYSTEMATIC DESCRIPTIONS

STEREOLASMA RECTUM (Hall)

Pl. 58, figs. 1–16

Strombodes? rectus Hall, 1843, p. 209, text-fig. 5, p. 210; Table of Organic Remains, no. 48, fig. 5.
Cyathophyllum rectum Edwards & Haime, 1851, p. 372.

EXPLANATION OF PLATE 58

All figures ×2

FIGS. *1–16*—*Stereolasma rectum* (Hall). *1–7*, Busch's hypotypes, OSU 18755 and 18754 a–f; *8–10*, syntypes of *Caninia complexa* Busch, OSU 18763 b–e; *11–15*, serial transverse sections of hypotype UMMP 36087; Wanakah shale, "demissa" bed, along Smoke Creek, 1½ miles south of Reserve, Erie Co., New York; *16*, longitudinal section of hypotype UMMP 36088, upper part of Wanakah shale, along banks of Smoke Creek at Windom, Erie Co., New York.

17–28,37–39—*Stewartophyllum intermittens* (Hall). *17–19*, Busch's hypotypes, OSU 18751 a–c; *20–24*, syntypes of *Barrandeophyllum reimanni* Busch, OSU 18768 b–f; *25–28*, syntypes of *Barrandeophyllum simplex* Busch, OSU 18771 b–d, f; *37–39*, syntypes of *Hapsiphyllum bifurcatum* Busch, OSU 18776 b–d.

29–32,40–50—*Amplexiphyllum hamiltoniae* (Hall). *29–32*, syntypes of *Caninia tabulata* Busch, OSU 18765b–e; *33–36*, Busch's hypotypes of *Amplexiphyllum hamiltoniae* (Hall), OSU 18759d,e,f, and h; *40–43*, syntypes of *Alleynia americana* Busch, OSU 18772a,d–f; *44–49*, serial sections of hypotype UMMP 36089, upper part of Wanakah shale along Smoke Creek, at Windom, Erie Co., New York; *50*, longitudinal section of hypotype UMMP 36090, coral layer of lower Windom shale along small stream at Athol Springs, Erie Co., New York.

Streptelasma recta Hall, 1876, pl. 19, figs. 1–13 *partim*.
Streptelasma ungula Hall, 1876, pl. 19, figs. 14–24 *partim*.
Stereolasma rectum Simpson, 1900, p. 205, text-figs. 16,17; Brown 1909, p. 67–71; Busch, 1941, p. 395, text-figs. 7–16; Stumm, 1959, p. 7, pl. 3, figs. 16–19; Hill, 1956, p. 257.
Caninia complexa Busch, 1941, p. 399, text-figs. 28–33.
Buschphyllum complexa Stumm, 1949, p. 9, pl. 3, figs. 37–39.

Description.—Corallites ceratoid to trochoid, ranging from 0.7 to 5 cm. in length and from 1 to 2.2 cm. in maximum diameter. Average diameter about 1.5 cm. Exterior with vertical interseptal ridges and faint, horizontal growth annulations spaced at various distances apart. Calyxes with thin erect walls and an axially sloping basal portion. Maximum depth of calyx 1.5 cm. Septa ranging from 48 to 60 of which the major extend to axis, where by addition of stereoplasm a stereocolumella is formed in the neanic and early ephebic growth stages. In the later ephebic growth stages columella ceases growth and major septa retreat from axis. Point of retreat typically just below base of calyx. Minor septa appear as short peripheral ridges at position where major septa retreat from axis. Tabulae relatively closely set, complete or incomplete, horizontal axially, distally convex periaxially, deflected proximally as they approach the periphery (see pl. 58, fig. 16). No dissepiments present.

Remarks.—The specimen showing dissepiments illustrated by Busch (1941, p. 400, text-fig. 33) is apparently a small specimen of a species of *Bethanyphyllum*. Busch's type of *Caninia complexa* (pl. 58, fig. 8) displays the stereocolumella characteristic of the neanic and early ephebic growth stages of *Stereolasma rectum*.

Occurrence.—Middle Devonian, Hamilton group, Ludlowville formation, Wanakah shale member; Moscow formation, Windom shale member, western New York.

Types.—The holotype illustrated by Hall (1843, p. 209, text-fig. 5) has not been traced. It may have been reillustrated by Hall (1876, pl. 19) but none of Hall's 1876 drawings exactly match the 1843 drawing. Of Hall's 1876 hypotypes, the originals of figs. 1,2,11,12,13 are in the American Museum of Natural History numbered 4464/1; of figs. 3,5,7,8 in the same institution numbered 4464/2; of fig. 9 in the New York State Museum numbered 3740/1. The originals of figs. 4,6,10 have not been traced. Some of Hall's 1876 hypotypes may be specimens of *Lopholasma carinatum* Simpson (1900, p. 206, text-figs. 19–20) but a tangential section must be made of each specimen in order to distinguish between the two species. Busch's hypotypes Ohio State University Geological Museum nos. 18754–18755; of *Caninia complexa* Busch no. 18673; hypotypes herein illustrated, University of Michigan Museum of Paleontology nos. 36087, 36088.

Amplexiphyllum hamiltoniae (Hall)
Pl. 58, figs. 29–32; 40–50

Streptelasma ungula Hall, 1876, pl. 19, figs. 14–24 *partim*.
Amplexus hamiltoniae Hall, 1876, pl. 19, figs. 20–23; Busch, 1941, p. 397–399, figs. 17–27.
Caninia tabulata Busch, 1941, p. 401–403, figs. 34–40.
Alleynia americana Busch, 1941, p. 407–408, figs. 56–63.
Amplexiphyllum hamiltoniae Stumm, 1949, p. 9, pl. 3, figs. 32–36; Hill, 1956, p. 257.

Description.—Typically ceratoid, rarely trochoid or subcylindrical corallites, many irregularly contorted. Maximum diameter observed 2.1 cm., diameter of average corallite about 1.6 cm. Exterior with relatively closely spaced growth annulations. Maximum length about 4 cm., average about 3 cm. Calyxes typically shallow, 3–5 mm. deep with sloping walls. Septa in neanic stage typically thick, rarely thin, becoming thinner toward distal ends, major septa extending to axis, minor septa appearing as peripheral ridges at a corallite diameter of 1.2 to 1.6 cm. Septa in different individuals ranging from 48 to 59. At a corallite diameter of 0.8 to 1 cm. major septa retreat from axis becoming increasingly shorter and thinner distally. Cardinal fossula represented by shortened cardinal septum in late neanic and ephebic stages. Tabulae, complete or incomplete, from 8 to 10 to a centimeter, typically horizontal axially, becoming deflected proximally as they approach the periphery in the majority of specimens. In some, the tabulae remain horizontal to the peripheral wall. No dissepiments present.

Remarks.—A study of serial sections of 12 corallites reveals that the septa vary

greatly in thickness. Serial sections of a specimen (pl. 58, figs. 44–49) show that the septa in the neanic stage are long and thick, but become progressively thinner and shorter in the ephebic stage. Number of septa of different specimens at the same corallite diameter are very similar. At a diameter of 1 cm. the septal count in 6 specimens is 21, 23, 26, 23, 20, and 25.

Occurrence.—Middle Devonian, Hamilton group, Ludlowville formation, upper Wanakah shale; Moscow formation, lower Windom shale, western New York.

Types.—Hall's syntypes (the originals of Hall's 1876, pl. 19, figs. 20–23) American Museum of Natural History no. 4441/1. Busch's hypotypes, Ohio State University Geological Museum no. 18759. Busch's types of *Caninia tabulata* no. 18765; of *Alleynia americana* no. 18772. Hypotypes herein illustrated University of Michigan Museum of Paleontology nos. 36089, 36090.

STEWARTOPHYLLUM INTERMITTENS (Hall)
Pl. 58, figs. 17–28,37–39

?Strombodes distortus Hall, 1843, p. 209, text-fig. 4; Table of Organic Remains, no. 48, fig. 4.
Strombodes? Hall, 1843, Table of Organic Remains, no. 49, figs. 2–2a.
Amplexus intermittens Hall, 1876, pl. 32, figs. 8–15.
Stewartophyllum intermittens Busch, 1941, p. 394–395, figs. 1–6; Stumm, 1949, p. 9, pl. 3, figs. 25–28; Hill, 1956, p. 257.
Barrandeophyllum reimanni Busch, 1941, p. 403–405, figs. 41–49.
Barrandeophyllum simplex Busch, 1941, p. 405, figs. 50–55.
Hapsiphyllum bifurcatum Busch, 1941, p. 409, figs. 64–73.

Description.—Corallum subcylindrical to ceratoid, typically with irregularly spaced flangelike expansions. Calyx relatively flat, peripheral area reflexed in some specimens. Cardinal fossula weakly to moderately well developed (see Hall, 1876, pl. 32, figs. 8–15). In transverse section of neanic stage septa from 16 to 18, thick, extending almost to axis. In early ephebic stage septa from 19 to 22, thick, extending almost to axis in most specimens but only two thirds distance to axis in others. Thick axial ends of septa in lateral contact produce appearance of aulos in a minority of the specimens. In late ephebic stage (just beneath base of calyx) septa extend about two-thirds distance to axis, typically with free axial ends. At this point the minor septa appear as short peripheral ridges. Cardinal fossula moderately to well developed. In longitudinal section the tabulae are complete and incomplete, relatively flat-topped axially. In the peripheral areas they may be deflected upward, downward, or remain horizontal. No dissepiments.

Remarks.—This form can be distinguished from *A. hamiltoniae* by the flangelike growth expansions on the exterior of the corallum, by the continuously thick and relatively long major septa from neanic to ephebic stage. The tabulae are similar to those of *A. hamiltoniae* except that they may be horizontal or deflected upward in the peripheral regions.

Occurrence.—Middle Devonian, Hamilton group, Ludlowville formation, upper Wanakah shale; Moscow formation, lower Windom shale, western New York.

Types.—Holotype of *Strombodes distortus* not located; syntypes of *Stewartophyllum intermittens* American Museum of Natural History 4442/1 and 4442/2; Busch's hypotypes Ohio State University Geological Museum 18751; of *B. reimanni* Ohio State University Geological Museum 18771, of *H. bifurcatum* Ohio State University Geological Museum 18776.

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JOURNAL OF PALEONTOLOGY, V. 35, NO. 3, P. 448–450, PLS. 59–60, MAY, 1961

BUSYCON (BUSYCON) TRITONE CONRAD REDESCRIBED AND REILLUSTRATED

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ABSTRACT—The previous literature pertaining to *Busycon* (*Busycon*) *tritone* Conrad is briefly reviewed and the species is redescribed and reillustrated on the basis of a well preserved topotype.

INTRODUCTION

IN AUGUST 1956 the writer collected an unusually well preserved specimen of *Busycon* (*Busycon*) *tritone* Conrad from the Upper Miocene Yorktown formation near Yorktown, Virginia. After searching the literature for a suitable description and illustrations of this species it became apparent that none was available. The species is rather common in the Yorktown and has been referred to by several authors in phylogenetic and comparative studies of the genus *Busycon* (Conrad, 1867a, p. 184; Conrad, 1867b, p. 265; Grabau, 1903, p. 530; Smith, 1905, p. 354–355; Gardner, 1948, p. 239).

Apparently Conrad originally considered *B.* (*B.*) *tritone* as a variety of *B.* (*B.*) *maximum* (Conrad, 1839; 1861, p. 83) and then in 1863 (p. 583) he described it as a new species. Four years later the first illustration was published (Conrad, 1867b, pl. 20, fig. 2). Subsequent authors have been undecided as to how to treat the species. Grabau (1903, p. 530) considered *B.* (*B.*) *tritone* a valid species. The usage of Smith (1905) is questionable; he also considered it valid (p. 354–355) but then illustrated a specimen (pl. 31, fig. 12) under the name *Fulgur maximum* which is here placed in synonymy with *B.* (*B.*) *tritone*. Then in 1948 Gardner (p. 239) noted the similarity between *B.* (*B.*) *tritone* and *B.* (*B.*) *maximum* but called attention to the fact that the peripheral sculpture of the former is spinose (tuberculated).

Since Conrad's type specimen of *B.* (*B.*) *tritone* at the Philadelphia Academy of Natural Sciences is very fragile and incomplete (Horace G. Richards, personal communication) the following description and illustrations are based upon a nearly complete topotype possessing certain features not mentioned in Conrad's original description.

SYSTEMATIC DESCRIPTION

Phylum MOLLUSCA
Class GASTROPODA
Order RACHIGLOSSA
Family BUSYCONIDAE

Genus BUSYCON

Busycon Röding, 1798, p. 149; Hollister, 1958, p. 68.
Fulgur Montfort, 1810, p. 503.

Type species.—*Murex aruanus* Linné, 1758, p. 753.

Diagnosis.—See Hollister, 1958, p. 68.

EXPLANATION OF PLATE 59

FIGS. *1,2*—*Busycon* (*Busycon*) *tritone* Conrad, *1*, ventral view showing anterior portion of major growth ornamentation sharply bent laterally and then posteriorly before disappearing under the parietal shield, ×1; *2*, right lateral view showing foliated tubercles and anterior elongate, elevated lip-like "flanges" on the major growth ornamentation, ×1, hypotype, UNSM 28.

1
2

1
2

BUSYCON (BUSYCON)

Diagnosis.—See Hollister, 1958, p. 70.

BUSYCON (BUSYCON) TRITONE Conrad

Pl. 59, figs. 1,2; pl. 60, figs. 1,2

?*Fulgur maximus* var. A Conrad, 1839, inside back cover.

?*Busycon maximum* var. A Conrad, 1861, p. 83 *non* pl. 47.

B. tritonis Conrad, 1863, p. 583; 1867b, p. 265, pl. 20, fig. 2.

Fulgur maximum Smith, 1905, pl. 31, fig. 12.

Busycon tritone Shimer & Shrock, 1944, pl. 206, fig. 14.

Redescription.—Shell large, heavy, subpyriform, dextral. Body whorl inflated posterior to mid-length and obtusely angulated posterior to greatest width. Aperture large, greatly enlongated anteriorly into an open siphonal canal and with an acute groove at the posterior end. Outer lip thin, flat to slightly concave above angulation, smoothly convex below, becoming gently sigmoid along the siphonal canal. Inner lip smoothly convex anteriorly becoming sinuous along the siphonal canal and with a smooth, wide parietal shield tightly appressed on the body whorl throughout its length.

Spire of five moderately elevated, scalariform whorls. Nucleus apparently of about one rounded whorl. Second whorl flat; third, fourth, and fifth whorls obtusely angulated. Sutures slightly impressed.

Revolving ornamentation of two types: (1) prominent, short, stubby, reflexed, trough shaped tubercles on the angulation of the body whorl which grade imperceptibly to low, rounded nodes on the first half of the penultimate whorl before disappearing, (2) numerous low, rounded spiral threads, widely spaced on the body whorl becoming more sharply crested and closely spaced on the spire before disappearing about two whorls ahead of the nucleus.

Growth ornamentation also of two types: (1) prominent, foliated, evenly and distantly spaced, raised, tuberculated ridges anteriorly elevated into elongate, reflexed "flanges" on the body whorl before bending sharply laterally and finally bending again sharply posteriorly before disappearing under the parietal shield, (2) numerous, barely perceptible, more closely spaced, low, rounded growth lines.

Remarks.—Although *Busycon* (*Busycon*) *maximum* Conrad, *sensu stricto* (see Conrad, 1861, pl. 47) and *B.* (*B.*) *tritone* Conrad are closely related they are not conspecific and may be easily distinguished by the presence of large tubercles on the peripheral angle of the latter. The specimen of *B.* (*B.*) *tritone* herein described apparently differs from Conrad's type in possessing conspicuously elevated, lip-like "flanges" on the major growth ornamentation toward the anterior portion of the body whorl. Such ornamentation was not described or illustrated by Conrad or any subsequent authors with the exception of Smith (1905, pl. 31, fig. 12, p. 361) who considered this to be a gerontic feature of *B.* (*B.*) *maximum*.

The early ontogenetic development of *B.* (*B.*) *tritone* remains unknown since the initial whorl of the specimen herein described is eroded.

Occurrence.—Upper Miocene, Yorktown formation. From the bluffs along the south bank of the York River, approximately one mile southeast of the Yorktown-Gloucester Point highway bridge, York County, Virginia.

Type.—Hypotype No. 28, University of Nebraska State Museum, Lincoln.

LITERATURE CITED

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EXPLANATION OF PLATE 60

FIGS. *1,2*—*Busycon* (*Busycon*) *tritone* Conrad, *1*, dorsal view showing revolving ornamentation, ×1; *2*, apical view showing partially eroded nucleus and reflexed tubercles, ×1, hypotype, UNSM 28.

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JOURNAL OF PALEONTOLOGY, V. 35, NO. 3, P. 451–456, PL. 61, 4 TEXT-FIGS., MAY, 1961

NEW TEREBRATULOID GENERA FROM AUSTRALIA

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ABSTRACT—Three new genera of terebratuloid brachiopods from the Permian of Australia have been recognized. These genera are here described as *Gilledia* with *Terebratula cymbaeformis* Morris 1845 as genotype, *Fletcherina* with *Terebratula amygdala* Dana 1847 as genotype, and *Yochelsonia* with a new species *Y. thomasi* as genotype. This investigation has included study of the internal structures of these forms and both serial sections and reconstructions of internal structures are provided.

INTRODUCTION

IN CONNECTION with studies undertaken for the *Treatise on Invertebrate Paleontology*, Mississippian, Pennsylvanian and Permian terebratuloid brachiopods have been assembled from all over the world. Consideration of the species obtained from Australia has resulted in the recognition of three previously undescribed genera. These three new genera are here described and figured. The writer wishes to express his thanks to G. A. Cooper, U. S. National Museum; H. Fletcher, the Australian Museum, Sidney; E. D. Gill, National Museum of Victoria, Melbourne; G. Thomas, Bureau of Mineral Resources, Canberra and K. S. W. Campbell, University of New England, Armidale, N.S.W., all of whom provided material or offered helpful suggestions.

Genus GILLEDIA Stehli, n. gen.
Text-figs. 1A,2

Genotype.—*Terebratula cymbaeformis* Morris, 1845, p. 278, pl. 17, figs. 4–5.

Diagnosis.—Large radially carinate Dielasmatidae in which the ventral valve is longitudinally convex but transversely almost flat or slightly sulcate. Dorsal valve longitudinally and transversely convex. Ventral interior with pedicle collar; dental plates present but united with wall of rostral cavity by callus deposit. Dorsal interior with the crural bases attached to the floor of the valve, but not united by the cardinal plate with the socket plate; cardinal plate medially sessile and so divided into two discrete plates; cardinalia overgrown with heavy callus deposits; loop broad, terebratuliform with main bands far apart.

Geologic range.—Wyro Stage, Wooramel Dist., W. Australia; Marine Series, Bowen River Coalfield, Queensland, Australia; Upper Marine Series, Wyro, near Ulladulla, N.S.W., Australia. Early Permian.

Geographic range.—Probably only from the Australian region.

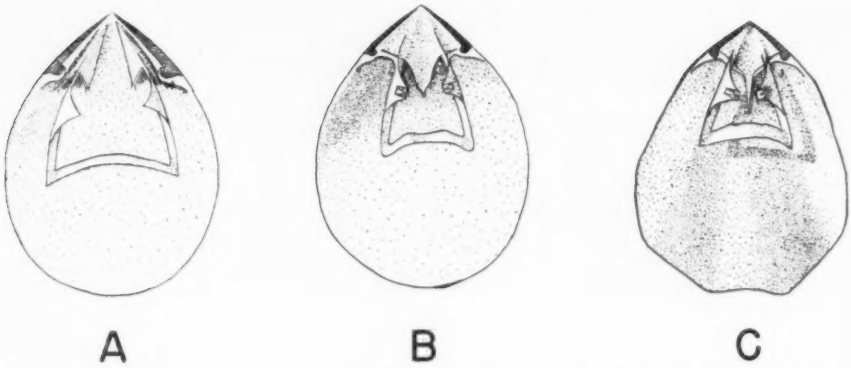
Discussion.—This genus is remarkable for its peculiar surface ornamentation which consists of a pattern, not unlike that of some recent members of the genus *Terebratulina*, except for waviness of the carinae. The carinae as in *Terebratulina* probably reflect the positions of setae in the mantle edge. Internally the excessive callus deposition tends to obscure the cardinalia but the basic elements as described above appear to be present.

Species assigned.—*Terebratula cymbaeformis* Morris, 1845, genotype and only known species.

GILLEDIA CYMBAEFORMIS (Morris)
Pl. 61, figs. 1–6

Terebratula cymbaeformis Morris, 1845, p. 378, pl. 17, figs. 4,5.
Terebratula sacculus cymbaeformis, de Koninck, 1877, p. 225, pl. 15, figs. 4–42.
Dielasma cymbaeformis, Etheridge, 1892, p. 225, pl. 9, figs. 10,11.

Diagnosis.—Shell large, ornamented by faint wavy radial carinae. Ventral valve moderately and rather evenly convex longitudinally; transversely with slight convexity posteriorly but becoming flat anteriorly; beak erect; foramen permesothyrid, labiate;



TEXT-FIG. 1—Diagrammatic reconstructions of the dorsal interior of A, *Gilledia*, and B, *Fletcherina*, both based on interpretation of serial sections and internal molds; C, *Yochelsonia* based on serial sections alone.

deltidial plates conjunct; beak ridges rounded. Dorsal valve longitudinally of low convexity; transversely of moderate to high convexity. Anterior commissure uniplicate; lateral commissure sinuate. Internal characteristics as described for the genus.

Remarks.—In his original description of this species, Morris (1845) figures only an internal mold. He therefore probably had no awareness of the peculiar carinate ornamentation so characteristic of the species. His figures clearly show, however, most of the characteristics found in the specimen sectioned during the present study and the writer is confident that the two specimens are conspecific.

Material.—One almost perfect specimen from Upper Marine series, Wyro, near Ulladulla, N.S.W. Australia, (C.I.T. 5951). Several internal molds, Woodbridge Glacial formation, Blackwood Ck. near Cressy, Tasmania (U. of Tasmania 25250).

Genus FLETCHERINA Stehli, n. gen.
Text-fig. 1B,3

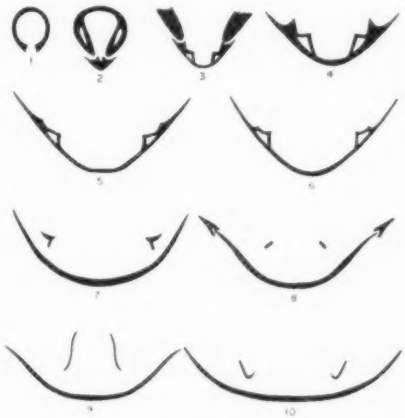
Genotype.—*Terebratula amygdala* Dana, 1847, p. 152.

Diagnosis.—Dielasmatidae externally homeomorphous with *Dielasma* but differing internally in the fusion of the two halves of the cardinal plate to form a prominent median septum, and in the possession of elongated crural points.

Geologic range.—Lower Permian.

Geographic range.—Presently known only from Australia.

Discussion.—The consistent union of the two halves of the cardinal plate in *Fletcherina* requires important soft part reorganiza-

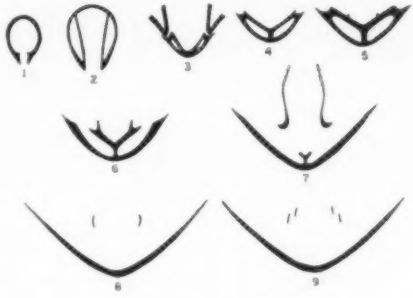


TEXT-FIG. 2—Idealized serial sections of *Gilledia*.

tion. This is principally manifest in the changed insertion site of the dorsal pedicle muscles which have had to rise from the valve floor to an elevated position thus producing differences in leverage and contractility. At the present time no genera have been described which appear to be descendent from *Fletcherina* and the secondary fusion of discrete cardinal plates may represent a brief and unsuccessful "experiment." It seems possible, though perhaps unlikely, that continuance of this trend could have produced a nearly plane secondary cardinal plate supported by a median septum. Obsolescence of the middle of the hinge plate could have produced the cardinalia characteristic of so many Mesozoic terebratuloids.

The variability in external form in this genus is considerably greater than that seen in the internal structures. *F. inversa* is strongly biplicate while *F. amygdala* is only incipiently biplicate or in many individuals even completely smooth.

Species assigned.—*Terebratula amygdala* Dana and *Rhynchonella inversa* de Koninck.



TEXT-FIG. 3—Idealized serial sections of *Fletcherina*.

FLETCHERINA AMYGDALA (Dana)
Pl. 61, figs. 7,10,11,14,15,19–22

Terebratula amygdala Dana, 1847, p. 152.

Diagnosis.—Shell of moderate size; externally indistinguishable from many species of *Dielasma* and *Beecheria* except for a tendency toward very faint biplication of the anterior commissure in some individuals. The color pattern consists of irregular radial bands. Internally the ventral valve shows dental plates and a pedicle collar. The dorsal interior, with the cardinal plates extending in a shallow "V" between the socket plates and supported by a double walled septum, formed from the union of the ancestrally discrete portions of a medially sessile cardinal plate; crura arising from the cardinal plate near its unions with the socket plates; crural points extremely long; loop short, terebratuliform.

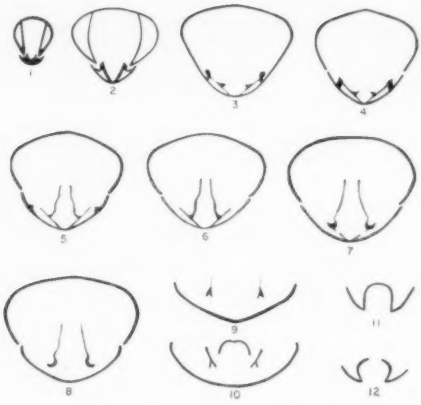
Remarks.—Externally this species appears to differ considerably from *F. inversa* because of the weakness of the plications which are sometimes developed and sometimes not. The tendency toward biplication together with the internal similarity seems to suggest that both species must be placed in the same genus however.

Material.—Four specimens, Upper Marine Series, Gerringong, N.S.W. Australia (C.I.T. 5956). Two specimens, "Permo-Carb" Greta, N.S.W. Australia (USNM 24474). Four specimens, Upper Marine Series, Gerringong, N.S.W. Australia (USNM 112142).

FLETCHERINA INVERSA (de Koninck)
Pl. 61, figs. 8,9,12,13,16,26

Rhynchonella inversa de Koninck, 1877, p. 171, pl. 11, fig. 11.
Dielasma inversa Etheridge, 1898, p. 175–6, pl. 19, figs. 1–13.

Diagnosis.—Moderate to large sized *Fletcherina*. Ventral valve longitudinally of moderate convexity which is strongest toward the beak, transversely of moderate convexity toward the beak but becoming flatter anteriorly; near or somewhat posterior to mid-length appears a median fold flanked by sulci which become more prominent toward the front; ventral beak erect; beak ridges rounded, foramen permesothyrid, labiate; deltidial plates conjunct. Dorsal valve of slight longitudinal convexity but of high transverse convexity; a median sulcus develops posterior to mid-length and is flanked by folds; a lesser sulcus and fold are present on the lateral slopes. Anterior commissure sulciplicate to episulcate; lateral commissures sinuate. Shell oval in outline; smooth or with concentric growth lines;



TEXT-FIG. 4—Idealized serial sections of *Yochelsonia*.

color pattern unknown. Interior as described for the genus.

Material.—Two specimens from Upper Marine Series, Wyro., near Ulladulla, New South Wales, Aust. One internal mold, Permo-Carboniferous, Greta, N.S.W., Aust. (C.I.T. 5954, 5955).

Genus YOCHELSONIA Stehli, n. gen.
Text-Fig. 1C,4

Diagnosis.—Small Dielasmatidae of subtriangular to pentagonal outline; ventral valve with a high median fold bordered by sulci; front and sides of both valves geniculate; dorsal valve longitudinally flat to concave with a pronounced median sulcus.

Ventral interior with well developed dental plates and a pedicle collar; muscles poorly impressed and their positions unknown. Dorsal interior with the cardinal plate medially sessile so as to appear as two separate plates extending from the socket plates to the valve floor; crura arising from these plates; plates becoming free of the sockets before they become free of the valve floor so that for a distance the crura are supported on a "V"; crural points developed to an extraordinary length; loop terebratuliform.

Geologic range.—Calceolispongia Stage, zones 29–32.

Geographic range.—Known only from the west side of the syncline south of Minilya River, Western Australia.

Discussion.—This genus was probably derived from such Salt Range species as "*Dielasma*" *biplex* Waagen by extreme alteration of the shape of the valves. The internal structures are very like those of "*Dielasma*" *biplex* and the basic pattern of a median ventral fold flanked by sulci and medially sulcate dorsal valve has also been retained. In detail the pattern of folding has been greatly exaggerated. The change in convexity of the valves and the modifications of the margins are features which place the genotype far outside the range of variability encompassed in "*D.*" *biplex* and closely related species, and *Yochelsonia thomasi* is therefore considered to represent a new genus. No descendant forms are known.

Species assigned.—*Yochelsonia thomasi* Stehli, n. sp.

YOCHELSONIA THOMASI Stehli, n. sp.
Pl. 61, figs. 17,18,23–25

Diagnosis.—Small dielasmatids of subtrigonal outline. Ventral valve of rather high longitudinal convexity especially near the beak; anterior margin geniculate; lateral margins geniculate, then the valve is flattened except for a high median fold which extends almost to the beak; beak erect; beak ridges slightly angular; deltidial plates conjunct; pedicle foramen permesothyrid. Dorsal valve longitudinally slightly concave; transversely of moderate convexity but with a pronounced median fold extending almost to the beak; front and sides of the valve geniculate. Shell smooth or with concentric growth lines especially on the geniculated margins. Color pattern unknown.

Ventral interior with dental plates and a pedicle collar; positions of muscle insertions uncertain. Dorsal valve with the cardinal plate medially sessile and descending unsupported from the socket plates to the valve floor; cardinal plates becoming free of the socket plates first; crura greatly elongated; loop terebratuliform.

Material.—Three specimens from Calceolispongia Stage zones 29–32; west side of

syncline south of Minilya River, Western Australia (U.S.N.M. 112685, 179050).

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ETHERIDGE, R., 1892, *in* JACK, R. L., & ETHERIDGE R., JR., Geology and Paleontology of Queensland and New Guinea: Geol. Survey of Queensland, pub. 92.

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MANUSCRIPT RECEIVED AUGUST 13, 1959

(*Explanation of Plate 61 will be found on page 456*)

EXPLANATION OF PLATE 61

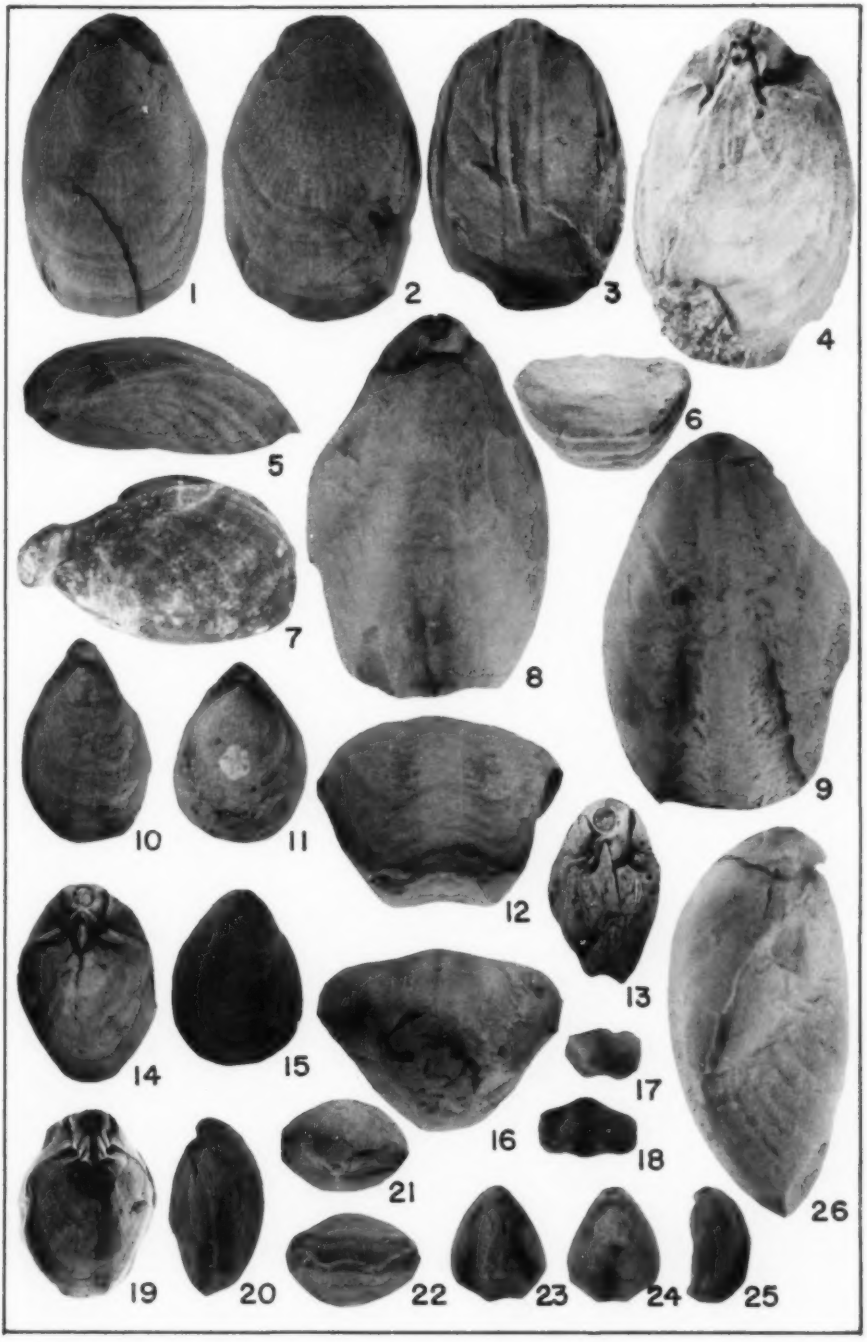
All figures ×1, except, as indicated.

FIGS. *1–6—Gilledia cymbaeformis* (Morris). *1*, dorsal exterior; *2*, ventral exterior, note wavy carinae; *3*, internal mold showing features of the interior of the pedicle valve, note impressions of the pallial sinus system; *4*, internal mold showing features of the dorsal interior, note positions of attachment of the secondarily thickened crural plates and sessile cardinal plates, ×1.3; *5*, profile, beak of ventral valve broken; *6*, anterior (California Institute of Technology 5951, Upper Marine Series, Wyro, near Ulladulla, N.S.W. Australia, 1,2,5,6; University of Tasmania 25250 Woodbridge glacial fm., Blackwood Ck. near Cressy, Tasmania, *3,4*).

7,10,11,14,15,19–22—Fletcherina amygdala (Dana). *7*, semiprofile of dorsal valve showing faint radial color markings ×1.5; *10*, dorsal exterior, note incipient plication of interior margin. Specimen with elongate ventral beak; *11*, dorsal exterior, specimen with normal beak and outline; *14*, internal mold showing impressions of internal structures of both valves; note impressions of pedicle collar and dental plates in ventral valve end of socket plates, median septum and medially depressed cardinal plate in dorsal valve; *15*, ventral exterior of specimen showing little tendency toward plication; *19*, rubber cast of internal mold of fig. 14, showing positive of internal structures noted; *20*, profile; *21*, posterior; *22*, anterior, showing plications (USNM 152877, Upper Marine Series, Gerringong, N.S.W. Australia,7,10,11,15, 19,20–22; USNM 24474, 14).

8,9,12,13,16,26—Fletcherina inversa (de Koninck). *8*, dorsal exterior; note plications characteristic of this species, ×2; *9*, Ventral exterior ×2; *12*, Anterior, ×2; *13*, Internal mold showing impressions of internal structures of both valves; note pedicle collar and dental plates in ventral valve and median septum and socket plates in the dorsal valve; *16*, posterior ×2; *26*, profile ×2, (California Institute of Technology 5954, Upper Marine Series, Wyro, near Ulladulla, N.S.W., Australia).

17,18,23–25—Yochelsonia thomasi, n. gen. et sp. *17*, posterior; *18*, anterior, showing geniculate margins; *23*, ventral exterior, showing the median fold and flanking sinuses; *24*, dorsal exterior showing deep median sulcus; *25*, profile showing the longitudinal flattening of the dorsal valve (USNM 179056, Calceolispongia Stage zones 29–32, west side of syncline south of Minilya River, Western Australia.)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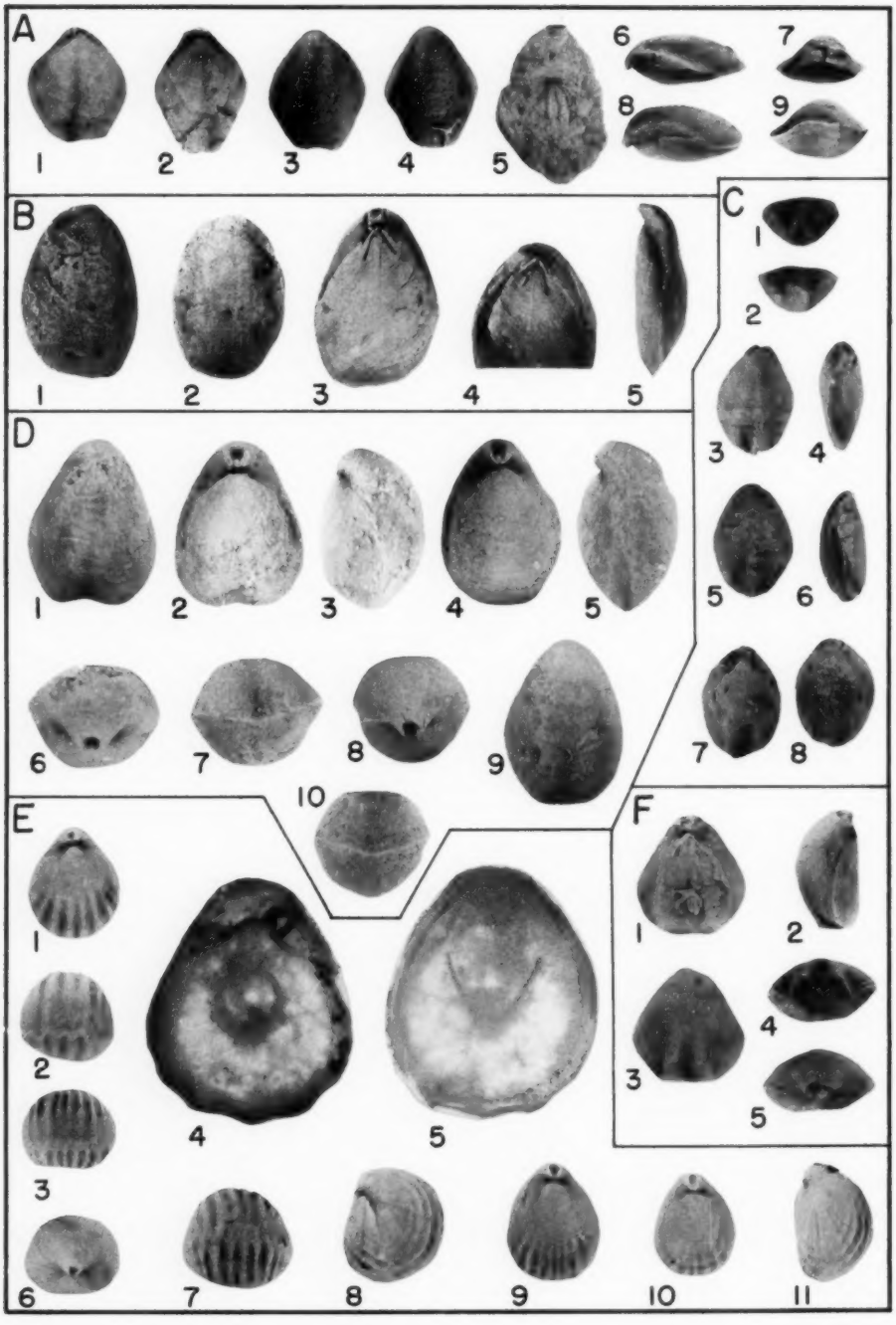
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JOURNAL OF PALEONTOLOGY, V. 35, NO. 3, P. 457–466, PL. 62, 8 TEXT-FIGS., MAY, 1961

NEW GENERA OF UPPER PALEOZOIC TEREBRATULOIDS

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ABSTRACT—Six new genera of terebratuloid brachiopods from Mississippian and Permian strata are described and figured. The new genera are *Gacina* with *G. cooperi*, n. sp., as genotype, *Afilasma* with *A. beecheri*, n. sp., as genotype, *Lowenstamia* with *L. texana*, n. sp., as genotype, *Pakistania* with *Dielasma biplex* Waagen as genotype, *Alwynia* with *Dielasma vesiculare* de Koninck as genotype and *Timorina* with *Notothyris minuta* Broili (non Waagen) as genotype. All of the available information regarding the internal characteristics of these forms is considered and diagrammatic reconstructions and idealized serial sections are presented.

INTRODUCTION

A STUDY of Paleozoic terebratuloid brachiopods was undertaken during the preparation of a chapter dealing with these fossils for the "Treatise on Invertebrate Paleontology." In the course of this study it became apparent that thanks to an excellent study by Cloud (1942) Silurian and Devonian terebratuloids were far better known than were their post-Devonian de-

EXPLANATION OF PLATE 62

Group A—*Gacina moorefieldensis* Stehli, n. sp. All specimens from Moorefield formation, NW ¼, NW ¼, sec. 18, T 15 N, R 21 E, 7 miles east, 1 mile south of Fort Gibson, Hulbert Township, Cherokee County, Oklahoma (USNM). All figures ×1 except as noted. *1*, Dorsal exterior showing the generally pentagonal outline of the valve and the pronounced dorsal sulcus; *2*, dorsal exterior of elongate individual indicating range of variation of species; *3*, ventral exterior showing pronounced ventral fold and the characteristic lateral flattenings of this valve; *4*, ventral exterior of more elongate specimen; *5*, specimen split to reveal a part of the loop and showing the closely spaced descending bands (×1.3); *6,8*, profile showing relief of ventral fold above lateral flattenings, and the curvature of the beak; *7,9*, anterior showing nature of the commissure.

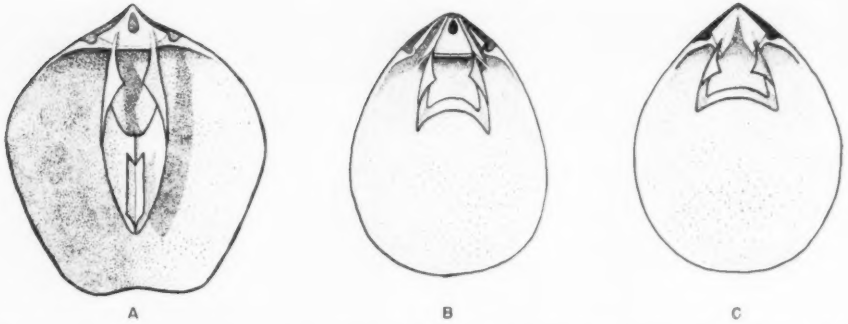
Group B—*Afilasma beecheri* Stehli, n. sp. All specimens from Chemung formation, Hornellsville, New York (Y.P.M.-S-1420). All figures ×1. *1*, Ventral exterior of the internal mold serving as holotype; *2*, ventral exterior of internal mold of paratype; *3*, dorsal exterior of holotype showing impressions of crural plate, apical foramen and socket plates in the dorsal valve and in the ventral valve the impression of dental plates and pedicle collar; *4*, latex impression of same specimen; *5*, profile of holotype.

Group C—*Pakistania schucherti* (Beede). All specimens from White Horse formation, White Horse Spring, Wood County, Oklahoma (Y.P.M-S-3699). All figures ×1. *1,2*, Anterior views showing the sulciplicate anterior commissure; *3,7*, dorsal exterior showing the median sulcus and the bordering folds; *4,6*, profiles; *5,8*, Ventral exteriors showing the median fold and bordering sulci.

Group D—*Lowenstamia texana* Stehli, n. sp. All specimens from Coleman Junction member of Putnam formation at San Angelo Junction, 4 miles SE of Coleman, Coleman County, Texas (C.I.T. 5965). All figures ×2½. *1,9*, Ventral exteriors showing variation in anterior outline; *2,4*, dorsal exteriors showing the strong, permesothyrid, labiate beak; *3,5*, profiles; *6,8*, posteriors; *7,10*, anteriors.

Group E—*Timorina broili* Stehli, n. sp. All specimens from Basleo, Timor, Dutch East Indies (C.I.T. 5963). *1,9,10*, Dorsal exteriors showing variable extention of plications onto valve (×2); *2,3,7*, anteriors showing the tendency toward development of a dorsal sulcus and ventral fold (×2); *4*, dorsal aspect of loop as seen in a prepared transparency with transmitted light; note the centronelliform aspect of the loop in this view (×4); *5*, ventral aspect of loop in transparency with transmitted light; note the two peculiar recurved bands arising from the vertical plate (×4); *6*, posterior (×2); *8,11*, profiles showing the strong longitudinal curvature of the ventral valve and the flattening of the dorsal valve (×2).

Group F—*Alwynia vesiculare* (de Koninck). Specimen from Carboniferous limestone series, Balladoole, Isle of Man, England (USNM 96998). All figures ×1½. *1*, Dorsal exterior showing the subpentagonal outline of the species; *2*, profile showing strong curvature of ventral valve and flattening of dorsal valve; *3*, ventral exterior showing the three sulci and two intervening folds; *4*, anterior showing the antiplicate nature of the commissure; *5*, posterior.



TEXT-FIG. 1—Diagrammatic reconstructions of the interior of the dorsal valve of (a) *Gacina*, (b) *Afilasma*, (c) *Lowenstamia*, based on serial sections and internal molds.

scendants. Investigation was therefore concentrated on Mississippian, Pennsylvanian and Permian forms and an attempt was made to obtain genotype material of all described genera and specimens of as many additional species as possible.

The incidence of external homeomorphy is high among terebratuloids and it was therefore considered necessary to investigate the internal structures of all species studied. This purpose was achieved by the use of silicified material, hollow specimens, prepared transparencies of calcite filled specimens, and when no other means were available, by the preparation of serial sections. These procedures resulted in the reinterpretation of many described genera and in the recognition of a number of new genera. It is the purpose of this note to describe new genera encountered.

The material studied in the course of this investigation was obtained from many parts of the world and it was inevitable that many individuals and institutions should have been called upon for help. It is a pleasure to acknowledge the helpful criticism, thought-provoking discussion and/or the materials generously supplied by the following: G. A. Cooper, U. S. National Museum; P. E. Cloud, U. S. Geological Survey; A. J. Boucot, Massachusetts Institute of Technology; C. O. Dunbar, Peabody Museum, Yale University; N. D. Newell, American Museum of Natural History; J. G. Ubaghs, Mineralogisch Geologisch Institut, Delft; H. A. Lowenstam, California Institute of Technology; and M. H. Khan, Geological Survey of Pakistan.

SYSTEMATIC PALEONTOLOGY

Genus GACINA Stehli, n. gen.

Text-figs. 1A,2

Genotype.—*Gacina moorefieldensis* Stehli, n. sp.

Diagnosis.—Terebratuloids of elongately sub-pentagonal to elliptical outline; much longer than wide. Ventral fold rather broad at the front and less pronounced than near mid-length where the margins of the valve tend to be flattened. Dorsal valve usually with a distinct sulcus extending almost to the beak.

Ventral interior with dental plates but without a pedicle collar. Dorsal interior with a free, perforate cardinal plate from which the crura arise; loop extending three-fourths the length of the valve; main bands uniting near mid-length and remaining so for the rest of their length; anteriorly a vertical plate develops; vertical plate antero-ventrally split to form incipient recurved bands.

Geologic range.—Onondagan?—Meramecian in N.A., Viséan in Europe.

Geographic range.—North America, Europe.

Discussions.—This genus is a link in the chain leading from a centronelliform loop type to the more or less cryptonelliform loops of related genera such as *Cryptacanthia* and *Glossothyropsis*. The loop is just begin-

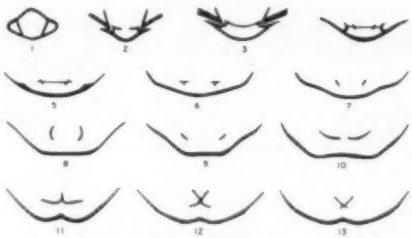
ning to develop recurved bands and probably supported a zugolophus lophophore in which the recurved portion was still very small. The position of the loop within the the valves is such that in view of the anterior union of the main bands it seems unlikely that the lophophore could have reached the more complex plectolophus stage. The recurved portion of the lophophore lay largely within the ventral valve for it must have been situated at the anteroventral margin of the split vertical plate. This development of the lophophore could have been one reason for the initial adoption of the sulcate condition found in this genus, for the high ventral fold would provide ample room. The anterior margin does not show pronounced breaks in the even curvature of its outline except as occasioned by the intersection of the fold and sulcus with the commissure, and it seems likely that there was slight anterior separation of the ends of the main bands of the lophophore and that they were directly supported by the split vertical plate.

The cardinalia have departed somewhat from the conservative centronellaceid pattern in the loss of the crural plates. Thus the free, perforate cardinal plate characteristic of closely related genera was already developed in *Gacina*. In the ventral valve, dental plates are well developed and this together with the nature of the cardinal plate suggests that *Gacina* did not arise from the externally similar Centronellinae but from some less specialized centronellaceid stock, possibly the Mutationellinae.

Species assigned.—*Gacina moorefieldensis* Stehli, n. sp.

Species questioned.—*Rhynchonella? alveata* Hall, 1857 p. 124. The internal characteristics of this species have not been determined as but a single specimen is known; however, its external similarity to other species of the genus leaves little doubt of its correct assignment. In view of the fact that only one specimen has ever been found, it seems possible that Hall incorrectly cited the collecting horizon and that it was actually taken from strata of Mississippian age.

Centronella emaciata Rowley, 1900, p. 265, pl. 5, figs. 48–50. The internal characteristics of this species have not been determined, but the external form is sufficiently distinctive to strongly suggest its assignment to *Gacina*.



TEXT-FIG. 2—Idealized serial sections of *Gacina*.

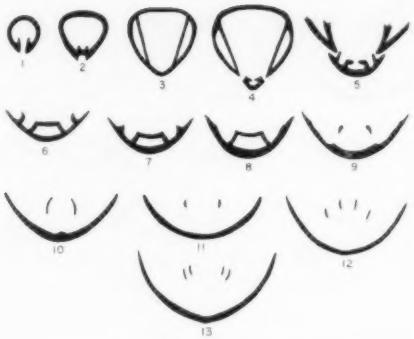
Rhynchonella reflexa de Koninck, 1887, p. 56, pl. 16, figs. 84–97. The internal characteristics are not known but the external form suggests placement here. The general shape suggests later genera of the group, however, and it is equally possible that it belongs to *Cryptacanthia* though if so it appears about 25 million years earlier than the next known representative.

GACINA MOOREFIELDENSIS Stehli, n. sp.
Pl. 62, group A, figs. 1–9

Diagnosis.—*Gacina* of moderate size. Ventral valve elongately pentagonal in outline; longitudinally strongly convex, more so near the beak; transversely with the convexity interrupted by a pronounced but rounded fold and, especially near midlength, by considerably flattened lateral margins; beak suberect; pedicle foramen mesothyrid, telate; deltidial plates conjunct. Dorsal valve pentagonal; longitudinally convex, but less so than the other valve; a pronounced but shallow sulcus arises immediately anterior to the beak and continues to the front. Interior as described for the genus.

Remarks.—This species differs from *Gacina? emaciata* in the presence of a pronounced sulcus in the dorsal valve. It differs from *Gacina? alveata* in its narrower, less deepened sulcus and more strongly flattened lateral areas. It may be distinguished from the Belgian species, *Gacina? reflexa* by the absence of a small median sulcus on the ventral fold.

Material.—Twenty specimens from the Moorefield fm. NW ¼, NW ¼, sec. 18,



TEXT-FIG. 3—Idealized serial sections of *Afilasma*.

T. 15 N., R. 21 E., 7 mi. E. and 1 mi. S. of Fort Gibson, Oklahoma (USNM). One internal mold from the Moorefield fm. on road to Bethesda, 6–7 mi. W. of Batesville, Ark. (USNM).

Genus AFILASMA Stehli, n. gen.
Text-figs. 1B,3

Genotype.—*Afilasma beecheri* Stehli, n. sp.

Diagnosis.—Moderate sized, terebratuliform shells, externally homeomorphous with *Cranaena*. Ventral interior with well developed dental plates and a pronounced pedicle collar. Dorsal interior with the cardinal plate free and apically perforate, extending between crural plates; cardinal plate obsolete between the crural plates and the socket plates; crura arising from the union of the cardinal plate and the crural plates; loop probably terebratuliform.

Geologic range.—Chemung (Upper Devonian).

Geographic range.—Known only from Hornellsville, New York.

Discussion.—This genus represents an early stage in the structural development of the important stock represented in the Mississippian by such species as *Beecheria chouteauensis* and *B. osceolensis* and in the Pennsylvanian by *B. bovidens*. It differs from these species in having a nonsessile, perforate cardinal plate. The genus probably arose from an early member of the Cranaeninae, possibly *Cranaena* itself by accelerated development of the crural bases under the cardinal plate. If so, the crural bases eventually united with the floor of the valve to form crural plates. The cardinal plate would then have become obsolete between the crural plates and the socket plates. Increasing concavity of the cardinal plate would have followed until sessility was achieved with the resultant formation of the discrete parts of the cardinal plate seen in the post-Devonian genus *Beecheria*. It is also possible, however, that the crural plates are primary and that this stock separated from the Cranaeninae before the latter lost crural plates.

Species assigned.—*Afilasma beecheri* genotype.

AFILASMA BEECHERI Stehli, n. sp.
Pl. 62, group B, figs. 1–5

Diagnosis.—Elliptical in outline, much longer than wide, anterior and lateral commissures rectimarginate. Ventral valve longitudinally mildly and evenly convex; transversely of low but regular convexity; beak erect, beak ridges slightly angular; foramen permesothyrid, labiate; deltidial plates conjunct. Dorsal valve longitudinally and transversely slightly convex.

Interiors of both valves as described for the genus.

Remarks.—The only two known specimens of this species are internal molds so nothing is known of the external details other than gross form. The characteristics of the ventral beak and the nature of the cardinalia place the genus unequivocally in close relationship to *Beecheria*. It was therefore considered, in view of its rarity, undesirable to sacrifice a specimen for sectioning. The terebratuliform loop has therefore not actually been seen, but is probably the only type that could have been present. The specimens do not show muscle scars.

Material.—This species is known from 2 specimens collected by C. E. Beecher from the Chemung at Hornellsville, N. Y., and now in the Schuchert Collection, Peabody Museum, Yale University, under the number Y.P.M.-S-1420. The better of the two specimens is designated as the holotype.

Genus LOWENSTAMIA Stehli, n. gen.
Text-figs. 1C,4

Genotype.—*Lowenstamia texana* Stehli, n. sp.

Diagnosis.—Small external homeomorphs of *Dielasma*, differing internally in the absence of dental plates and in the increasing obsolescence of the cardinal plates between the crural bases and the valve floor as they are traced anteriorly.

Geologic range.—Wolfcampian (Coleman Junction ls. member of Putnam fm.).

Geographic range.—Known only from Coleman, Texas.

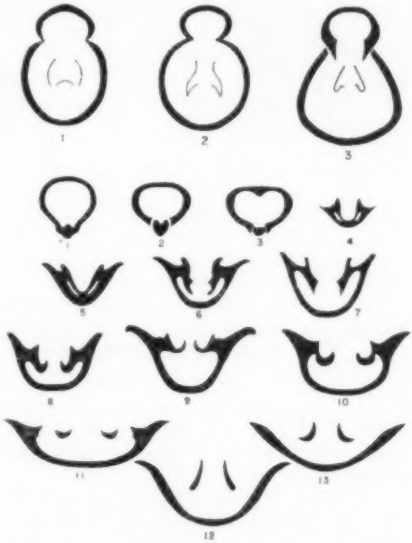
Discussion.—This small, rare genus is clearly a member of the Dielasmatinae as is shown by the permesothyrid, labiate beak, pedicle collar, loop and cardinalia. The loss of dental plates is a rather common occurrence in the more advanced genera of many lines. The appearance of a tendency toward obsolescence of the cardinal plates between the crural bases and the valve floor is, however, unusual and extremely interesting. Many Mesozoic terebratuloids possess a divided hinge plate with the crura arising from the inner wall of the socket plate. The development seen in *Lowenstamia* suggests a structurally possible means by which the common Mesozoic type of cardinalia could have arisen. Some Mesozoic forms having the divided hinge plate possess dental plates however, and it seems improbable that *Lowenstamia* is directly ancestral to any of them. It is considered more probable that the Mesozoic divided hinge plate arose from the Pseudodielasmatinae rather than from the Dielasmatinae, but the latter possibility can not be overlooked.

The interior of *Lowenstamia* is known only from serial sections but these reveal the loop in considerable detail and clearly show it to be of the terebratuliform type believed to have been associated with a plectolophus lophophore. It would be very interesting to know the position of insertion of the dorsal pedicle muscles, but unfortunately this can not be positively determined in the material studied. It seems probable, however, that they were inserted on the floor of the valve.

Species assigned.—*Lowenstamia texana* Stehli, n. sp. (genotype).

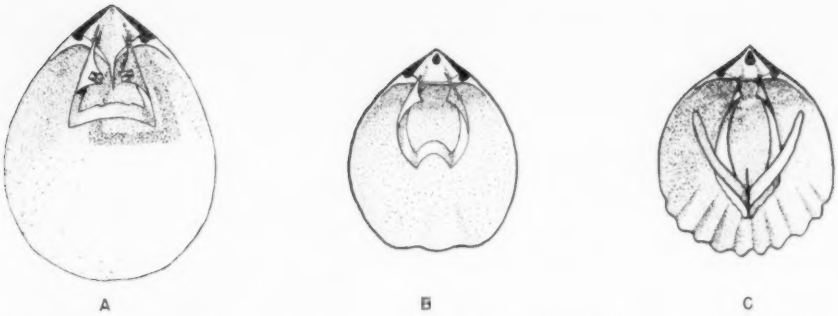
LOWENSTAMIA TEXANA Stehli, n. sp.
Pl. 62, group D, figs. 1–10

Diagnosis.—Small, smooth, rather inflated Dielasmatinae. Ventral valve longitudinally strongly and evenly convex, transversely evenly convex posteriorly, but anteriorly with a shallow median sulcus; beak erect to slightly incurved, beak ridges rounded; foramen permesothyrid, labiate; deltidial plates conjunct. Dorsal valve of strong longitudinal and transverse convexity. Lateral commissure nearly straight, anterior commisure gently uniplicate. Color pattern unknown.



TEXT-FIG. 4—Idealized serial sections of *Lowenstamia*, Top row, longitudinal sections (1–3), Cross sections seen in 1–13.

Ventral interior with a pedicle collar, without dental plates; position of muscle insertions uncertain. Dorsal interior with the cardinal plates medially sessile so that it appears to be divided into two independent plates extending from the sockets to the floor of the valve posteriorly; anteriorly the cardinal plates become free of the floor as the crural bases appear and then disappear between crural bases and the floor so that the crura are supported by small plates extending into the dorsal valve from the socket plates; this plate gradually becomes "U" shaped and then disappears as the crura become free of the sockets; a small scar is present at the apex of the valve for diductor attachment; placement of other



TEXT-FIG. 5—Diagrammatic reconstructions of the interior of the dorsal valve of (a) *Pakistania*, (b) *Alwynia*, (c) *Timorina* based on serial sections and transparencies.

muscles uncertain but probably as for subfamily; crural points normal; loop terebratuliform, with the transverse band rather strongly recurved.

Material.—Fifty specimens from the Coleman Junction ls. member of the Putnam formation at San Angelo Junction, 4 miles SE of Coleman, Coleman Co. Texas. (C.I.T. 5965).

Genus PAKISTANIA Stehli, n. gen.
Text-figs. 5A,6

Genotype.—*Dielasma biplex* Waagen, 1882, p. 249, pl. 25, figs. 3–5.

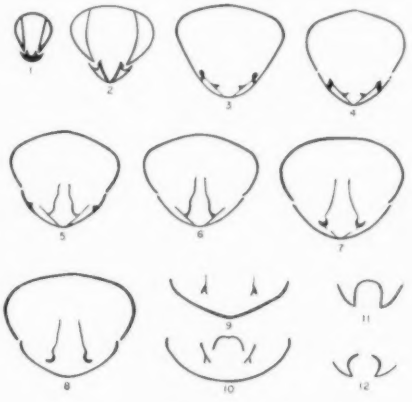
Diagnosis.—Medium to large terebratuliform Dielasmatidae of subpentagonal to ovate outline, with a sulciplicate anterior commissure. Ventral valve of moderate longitudinal convexity, transversely of low to moderate convexity, a median fold bordered by sulci appears a variable distance posterior to the front; ventral beak erect to slightly incurved; pedicle foramen permesothyrid, labiate; beak ridges rounded; deltidial plates conjunct. Dorsal valve of low longitudinal convexity, transversely of moderate convexity; a median sulcus notches the fold a variable distance anterior to the beak; the lateral slopes of the valve vary from convex to mildly concave. Lateral commissure sinuate.

Ventral interior with well developed dental plates and a pedicle collar; muscles poorly impressed and their positions unknown. Dorsal interior with the cardinal plates medially sessile so as to appear as two separate plates extending from the socket plates to the valve floor; crura arising from these plates; plates becoming free of the sockets long before the floor so that for a distance the crura are supported on a "V"; crural points developed to an extraordinary length; loop terebratuliform.

Geologic range.—Permian.

Geographic range.—Oklahoma, U. S. A.; Salt Range, Pakistan; Timor, Dutch East Indies; near Palermo, Sicily.

Discussion.—*Pakistania* is evidently related to *Dielasma* from which it was probably derived by the development of its characteristic sulciplicate anterior com-



TEXT-FIG. 6—Idealized serial sections of *Pakistania*.

missure and by the excessive lengthening of the crural points. The loop is of such a nature as to suggest the presence, in life, of a plectolophus lophophore. A small apical flattening or rudimentary cardinal process is present in the dorsal valve for the insertion of the diductor muscles. In the same valve the anterior and posterior adductors are more reasonably designated median and lateral. The median pair are represented by elliptical scars while lateral scars adjoin those but are longer, narrower, and located just anterior to and at the sides of the cardinal plates. The dorsal pedicle muscles are inserted on the floor of the valve between the sessile cardinal plates. The positions of individual muscle scars in the ventral valve are unknown.

In external form this genus is rather varied in detail though basic subfamily characters as well as the sulciplicate anterior commissure are always present. The folding may be limited to the immediate vicinity of the front or may extend far toward the umbonal region. Differences in the general convexity of the two valves are commonly found between species.

The exact relationships of *Pakistania* to the other genera of the sulciplicate complex with which it is associated can not now be determined. This is largely because of the imperfectly known age of the beds at some of the collecting localities. It is thus impossible to determine with confidence the temporal relationship of various genera. The mode of folding found in *Pakistania* is extremely common among Triassic and later terebratuloids and suggests relationship, yet it is difficult to see how the cardinalia of the Paleozoic and Mesozoic forms can be homologized. The most closely related genus appears to be *Yochelsonia* which is internally almost identical but differs externally in the nature of the folding.

Species assigned.—*Dielasma biplex* Waagen 1882, p. 249, pl. 25, figs. 3–5.

Dielasma schucherti Beede, 1902, p. 7, pl. 1, figs. 1–16.

Species questionably assigned.—*Dielasma acutangulum* Waagen, 1882, p. 353, pl. 26, figs. 1,2, fig. 7. The specimen figured by Waagen in his pl. 25, fig. 7, shows the characteristic internal features of the genus with the exception of the loop, and a rather definite assignment to *Pakistania* can be made.

Dielasma breviplicatum Waagen, 1882, p. 356, pl. 25, figs. 6,8; pl. 30, figs. 11,12. The specimen figured in pl. 25, fig. 8, shows the internal features of *Pakistania* with the exception of the loop, and crural points. The latter may have been reduced in length by breakage.

Dielasma problematicum Waagen 1882, p. 351, pl. 26, figs. 3,4. This species almost certainly belongs here but a positive assignment can not be made without a knowledge of internal details which is lacking.

Pakistania biplex (Waagen)

Dielasma biplex Waagen, 1882, p. 349, pl. 25, figs. 3–5.

Diagnosis.—Large *Pakistania* of pentagonal outline. Ventral valve of moderate longitudinal and transverse convexity; median fold strong, beginning just anterior to the beak and gaining adjoining sulci before half length; beak slightly incurved. Dorsal valve longitudinally almost a plane, transversely sharply convex; median sulcus and flanking folds beginning posterior to midlength; lateral slopes of valve strongly concave. Lateral commissure strongly sinuate. Growth lines infrequent. Color pattern unknown. Interiors characteristic for the genus.

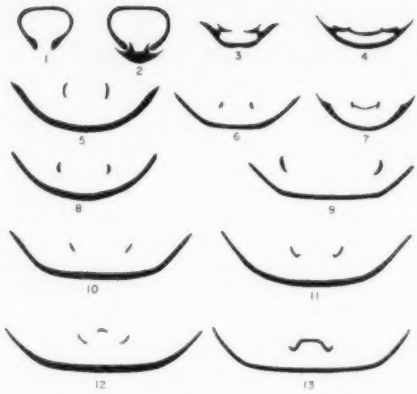
Comparison.—*Pakistania biplex* may be told from other probable species of the genus by its large size, prominent folding, and by the concave lateral slopes of the dorsal valve.

Material.—Two specimens from Mohra, Salt Range, Pakistan. Two specimens from the Salt Range, Punjab (C.I.T., 5961).

Pakistania schucherti (Beede)
Pl. 62, group C, figs. 1–8

Dielasma schucherti Beede, 1902, p. 7, pl. 1, figs. 1–16.

Diagnosis.—Small *Pakistania* of subpentagonal to oval outline. Ventral valve of low longitudinal convexity, transversely of low convexity near the umbo and becoming almost flat anteriorly; median fold and adjoining sulci low and appearing only near the front; beak erect. Dorsal valve of low longitudinal and moderate transverse convexity; median sulcus and adjoining



TEXT-FIG. 7—Idealized serial sections of *Alwynia*.

folds low and appearing only near the front. Lateral commissure slightly sinuate. Shell generally without concentric growth lines. Color pattern unknown. Internal structures as described for the genus.

Remarks.—Specimens of this species have been obtained only from the White Horse sandstone of Guadalupian age near White Horse Spring, Okla. Preservation is as internal molds on which most internal characters are well seen.

Comparison.—*Pakistania schucherti* may be distinguished from other species by its small size and by the low transverse convexity of the ventral valve. The convexity of the lateral slopes of dorsal valve is also useful in separating it from *P. biplex*.

Material.—Sixteen topotype specimens from White Horse Spring, Wood County, Oklahoma. (Y.P.M.-S-3699).

Genus ALWYNIA Stehli, n. gen.
Text-figs. 5B,7

Genotype.—*Dielasma vesiculare* de Koninck, 1887, p. 30, pl. 8, figs. 23–43.

Diagnosis.—Small Dielasmatidae with an antiplicate anterior commissure; ventral valve with two folds separated medially and bounded laterally by sulci; dorsal valve with little pronounced folding; pedicle foramen permesothyrid, labiate. Ventral interior with a pedicle collar, but without dental plates. Dorsal interior with a perforate cardinal plate extending unsupported between the socket ridges. Loop short, but modified from a typical terebratuliform condition by the close approach of the main bands anteriorly and the small transverse band.

Geologic range.—Viséan (Mississippian).

Geographic range.—Belgium and England.

Discussion.—This genus appears to occupy a position intermediate in the evolutionary sequence between the Cranaeninae and the group which includes *Rostranteris*. The absence of dental plates and the nature of the folding suggest relationship to *Rostranteris*. The nature of the cardinal plate is similar to that of both groups. The loop is clearly of a modified terebratuliform type but comparison with early ontogenetic stages in the loop of *Girtyella* suggests that its peculiar nature is due to a paedomorphic tendency. This again suggests relationship to *Rostranteris* and *Notothyris* in which the loop is clearly paedomorphic, never passing beyond the centronelliform stage.

The appearance in the Mississippian of a form closely allied to genera otherwise known only from the Permian points to the fact that our knowledge of Mississippian and Pennsylvanian forms is peculiarly incomplete. This gap in our knowledge is probably due to facies control, for the English and Belgian Viséan contain in *Gacina? reflexa* (de Koninck) at least one other terebratuloid unknown elsewhere and suggestive of later Pennsylvanian and Permian forms. It is to be expected that collecting from the Mississippian and Pennsylvanian will eventually yield forms more definitely linking *Alwynia* to the Permian members of the group of *Rostranteris*.

Species assigned. Dielasma vesiculare de Koninck, 1887.

Alwynia vesiculare (de Koninck)
Pl. 62, Group F, figs. 1–5

Dielasma vesiculare de Koninck, 1887, p. 30, pl. 8, figs. 23–43.

Diagnosis.—Small smooth Dielasmatidae of suboval outline in which the ventral valve is longitudinally and transversely convex while the dorsal valve tends to be flattened in both directions, but is somewhat curved at the margins. Ventral valve with two high sharp folds beginning near mid-length and

separated and laterally bounded by sharp sulci. Dorsal valve with folding reduced over most of the valve and evident only near the front. Anterior commissure antiplicate. Ventral beak slightly incurved; pedicle foramen permesothyrid and labiate. Anterior margin usually rather straight. Nature of color pattern, if any, unknown. Interior known only from serial sections and as described for the genus.

Material.—Three specimens from the Carboniferous limestone series, Balladoole, Isle of Man, England. USNM 96998.

Genus TIMORINA Stehli, n. gen.
Text-figs. 5C,8

Genotype.—*Notothyris minuta*, Broili, 1916, p. 68–70, pl. 127, figs. 22–29 (non Waagen 1882).

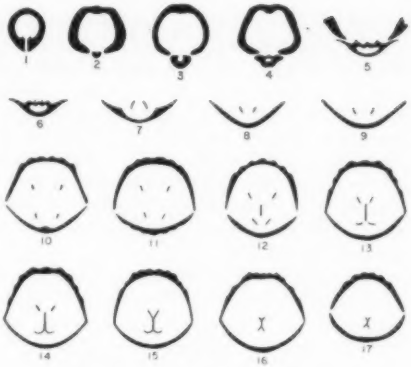
Diagnosis.—Small, biconvex, abundantly plicate, ellipitical in outline; anterior commissure tending toward sulcation. Ventral interior with a pedicle collar, without dental plates. Dorsal interior with a free, perforate cardinal plate from which the crura arise; crural points short; main bands of loop uniting in centronelliform fashion and forming a vertical plate; recurved bands arising from vertical plate and running anterolaterally to an abrupt ending.

Geologic range.—Middle Permian.

Geographic range.—Timor, Dutch East Indies.

Discussion.—Except for the unusual nature of the loop in *Timorina* it deviates little from the characteristic pattern of *Notothyris*. It seems beyond doubt that the genus arose either from *Notothyris* or from a closely related but unknown genus. Increasing complexity of the lophophore is an important and common trend in Paleozoic terebratuloids. *Timorina* is placed with the more conservative and typical forms, *Notothyris* and *Rostranteris*, despite its peculiar lophophore and loop.

This genus shows again the evolution of a long loop from a centronelliform loop which occurred in the Terebratellacea and some members of the Centronellacea. It is worth noting that this development of the long loop in the Permian comes just prior to the development of undoubted terebratellaceans in the Triassic. The only features of the loop distinguishing *Timorina* from the terebratuloids are the absence of a union of the loop with a median septum attached to the floor of the dorsal valve, the absence of a transverse connection between the recurved bands, and the failure of the main bands to separate anteriorly. It is perhaps unlikely that such a completely long looped stage was ever reached by this genus or its derivatives but it can not yet be shown to be impossible. Two methods would seem possible for the development of a septum uniting the dorsal valve and the loop. One would be the development of a septum beneath the cardinal plate and its gradual anterior extension. This seems improbable as there is no trace of such a development in any known member of the group. The second would be the development of an extension of the vertical plate of the loop toward the dorsal valve. This also seems doubtful for the vertical plate is itself formed by the union of the main bands of the loop as they bend away from the dorsal valve.



TEXT-FIG. 8—Idealized serial sections of *Timorina*.

Species assigned.—*Timorina broili.*

TIMORINA BROILI Stehli, n. sp.
Pl. 62, Group E, figs. 1–11

Notothyris minuta, Broili, 1916, p. 69–70, pl. 127, figs. 22–29 (non Waagen 1882).

Diagnosis.—A small, biconvex species of ellipitical outline. Ventral valve longitudinally and transversely of high, rather even convexity; beak short, inflated; beak ridges rounded; foramen permesothyrid, labiate,

deltidial plates conjunct; beak smooth with plications beginning a variable distance in front of it; plications extremely variable in number; medial two, three or more raised into a faint fold. Dorsal valve longitudinally and transversely convex but much less so than the ventral valve; umbo smooth with plications usually confined to the anterior margin where a faint sulcus includes a variable number. Internal characters as described for the genus.

Remarks.—Broili (1916, p. 70) has noted that in material from Timor which he assigned to *Notothyris minuta* Waagen the number and coarseness of the plications is highly variable. A collection of 84 specimens from Timor examined in the course of this study shows complete gradation between the characters ascribed by Waagen (1882) to *Notothyris minuta* and *Notothyris multiplicata*. It also showed, however, that both *N. minuta* and *N. multiplicata* of Waagen differ importantly in the structure of the loop from *N. minuta* of Broili. *Notothyris minuta* and *Timorina broili* are very close external homeomorphs but internally distinct.

Material.—Eighty-four specimens from Basleo, Timor, (C.I.T. 5963). Holotype: C.I.T. 5963:1.

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NEW GENERA AND SUBGENERA OF JURASSIC (BAJOCIAN) AMMONITES FROM ALASKA[1]

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ABSTRACT—New genera and species of Bajocian ammonites from Alaska include *Megasphaeroceras rotundum* Imlay, *Dettermanites vigorosus* Imlay, and *Parabigotites crassicostatus* Imlay. A new subgenus and species is *Oppelia* (*Liroxyites*) *kellumi* Imlay. Of these *Megasphaeroceras*, *Dettermanites* and *Oppelia* (*Liroxyites*) are associated with *Spiroceras*? *Leptosphinctes*, and *Sphaeroceras* of late Bajocian age. *Parabigotites* is associated with *Stephanoceras*, *Otoites*, *Sonninia*, *Witchellia* and *Lissoceras* of middle Bajocian age.

INTRODUCTION

STUDIES of the Middle Jurassic (Bajocian) ammonites from Alaska have shown that some of them belong to new genera and subgenera. These are validated herein in order that the names may be used in stratigraphic papers now being prepared by members of the U. S. Geological Survey. The type specimens are deposited in the collections of the U. S. National Museum. All localities are listed in the USGS Mesozoic locality catalog.

FOSSILS AND CORRELATIONS

Parabigotites crassicostatus Imlay, n. sp. has been referred previously to *Dactylioceras*? (Martin, 1926, p. 190), *Dactylioceras* (Kellum and others, 1945) and *Leptosphinctes* (Imlay, 1952, p. 979). Near Wide Bay in the Alaska Peninsula it occurs in the upper part of the Kialagvik formation. On the north side of Cook Inlet it occurs in the upper part of the siltstone below the Gaikema sandstone member of the Tuxedni formation. In the Talkeetna Mountains it occurs in the lower part of the Tuxedni formation equivalents. It is commonly associated with the ammonite *Stephanoceras* and locally with *Otoites*, *Sonninia*, *Witchellia* and *Lissoceras*. This association indicates an age equivalent to the *Otoites sauzei* zone of Europe.

Oppelia (*Liroxyites*) *kellumi* Imlay, n. sp., *Megasphaeroceras rotundum* Imlay, n. sp., and *Dettermanites vigorosus* Imlay, n. sp. are the common ammonites in the lower part of the Bowser member of the Tuxedni formation on the north side of the Cook Inlet region, Alaska. They show considerable resemblance to *Oppelia* (*Oxycerites*), *Sphaeroceras*, and *Polyplectites* respectively and in reports to field parties have been referred to those subgenera and genera. Because of those resemblances the lower part of the Bowser member has been correlated with the upper Bajocian of Europe (Imlay, 1952, p. 980) on the basis that *Oxycerites* and *Polyplectites* are not known from beds older than the upper Bajocian, and that *Sphaeroceras* is not known above the Bajocian.

This dating still stands, even though the ammonites in question are now assigned to new genera and subgenera and hence are of minor value for correlations with Europe. The evidence consists in part of the presence of *Spiroceras*? (Mes. loc. 21282), of a new species of *Sphaeroceras* (Mes. loc. 8572) and of several specimens of *Leptosphinctes* (Mes. locs. 21313, 21314, 21318) similar to *L. vermiformis* Buckman (1920, p. 162), *L. glyphus* (Buckman) (1925, pl. 544), and *L. davidsoni* Buckman (1921, pl. 201). Of these *Spiroceras* ranges from the upper Bajocian to the upper Bathonian (Arkell, 1957, p. L206), *Sphaeroceras* ranges from the zone of *Stephanoceras humphriesianum* to the end of the Bajocian (Westermann, 1956, p. 24–35; Arkell, 1952, p. 77; Arkell, 1956, p. 32,50, 142,268) and *Leptosphinctes* in Europe is typically upper Bajocian. There is a possible occurrence of *Leptosphinctes*, or of a closely related genus, in the middle Bajocian of Argentina (Jaworski 1926, pl. 13, fig. 8; Westermann, 1956, p. 268; Arkell, 1956, p.

[1] Publication authorized by the Director, U. S. Geological Survey.

585), but the report of *Leptosphinctes* in the middle Bajocian of Alaska (Imlay, 1952, p. 979) was based on specimens that are herein referred to a new genus *Parabigotites*.

Other evidence for correlating the lower part of the Bowser member of the Tuxedni formation with the upper Bajocian rather than with the middle Bajocian consists of the absence in it of any middle Bajocian ammonites such as occur in the underlying members of the Tuxedni formation. Thus the immediately underlying Cynthia Falls sandstone member contains *Chondroceras* and *Normannites* and the next underlying unnamed siltstone member contains these genera plus *Teloceras*, *Zemistephanus*, *Stephanoceras*, *Oppelia* (*Oppelia*), *Witchellia* and *Sonninia*. Most probably some of these genera would occur in the Bowser member, if it were as old as middle Bajocian.

U.S.G.S. MESOZOIC LOCALITIES

8572 G. C. Martin, 1913. Talkeetna Mountains at altitude of 4200 feet on ridge west of creek that enters the main Boulder Creek from the north 3 miles above its junction with the East Fork. Tuxedni formation equivalent.

11034 A. A. Baker, 1921. Insikin Peninsula on right fork of Cliff Creek 2.46 miles S. 15.5° W of mouth of Fitz Creek. Boswer member of Tuxedni formation about 100 feet above base.

11035 A. A. Baker, 1921. Iniskin Peninsula on right fork of Cliff Creek 2.68 miles S 16° W of mouth of Fitz Creek. Bowser member of Tuxedni formation, lower part.

11036 A. A. Baker, 1921. Iniskin Peninsula on right fork of Cliff Creek 2.58 miles S 15° W of mouth of Fitz Creek. Bowser member of Tuxedni formation, 125 to 175 feet above base.

11352 W. R. Smith, 1922. Wide Bay, 1 mile up creek southwest of Short Creek. Kialagvik formation, upper part.

12404 W. R. Smith, 1924. Wide Bay, southeast side of head. Kialagvik formation, upper part.

19773 L. B. Kellum, 1944. Wide Bay, 6.21 miles S 88° W of west end of Hartman Island. Kialagvik formation, about 225 feet below top.

19796 S. N. Daviess, 1944. Wide Bay. Float from bluff along southeast shore, 4 miles S 74½° E of Mt. Alai. Kialagvik formation, upper part.

19800 S. N. Daviess, 1944. Wide Bay, 4.2 miles due south of Mt. Alai at elevation of 1025 feet. Kialagvik formation, upper part.

19811 L. B. Kellum, 1945. Wide Bay, 6.55 miles S 56° W of west end of Hartman Island at elevation of 134 feet. Kialagvik formation, 45 feet below top.

19824 L. B. Kellum, 1945, Wide Bay, 5.9 miles S 54° W of west end of Hartman Island at elevation of 170 feet. Kialagvik formation, near top.

19934 Helmuth Wedow, Jr., 1944, Iniskin Peninsula, small tributary on right side of Cliff Creek, 2.42 miles S 14° W of mouth of Fitz Creek. Bowser member of the Tuxedni formation, about 85 feet above base.

19943 Helmuth Wedow, Jr., 1944. Iniskin Peninsula, on Cliff Creek 1¼ miles above junction with Fitz Creek and 3.35 miles east of Tonnie Peak. Bowser member of the Tuxedni formation, 125 to 175 feet above base.

19966 Helmuth Wedow, Jr. and L. B. Kellum, 1944. Iniskin Peninsula, north side of Gaikema Creek, one mile N 80° W of mouth of Fitz Creek. Siltstone about 850

EXPLANATION OF PLATE 63

All figures natural size unless otherwise indicated

FIGS. *1–4,6*—*Megasphaeroceras rotundum* Imlay, n. sp. *1*, paratype, USNM 130899a showing sharp ribbing of an immature form. *2,3,6*, holotype USNM 130898. Suture-line (×2) drawn at whorl height of 31 mm. Note smoothness of internal mold. *4*, paratype USNM 130899b showing sharp ribbing where the shell is preserved and apertural constriction and contraction. All specimens from USGS Mes. loc. 21314.

5,7–9—*Oppelia* (*Liroxyites*) *kellumi* Imlay, n. sp. *5*, paratype, USNM 130889a from USGS Mes. loc. 21318. Suture-line (×2) drawn at whorl height of 15.5 mm. *7*, ventral view of paratype USNM 130888 from USGS Mes. loc. 19943. *8*. holotype USNM 130886 from USGS Mes. loc. 2001 showing adult body chamber. *9*, paratype USNM 130887a from USGS Mes. loc. 20001 showing adult body chamber.

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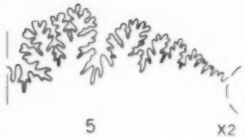

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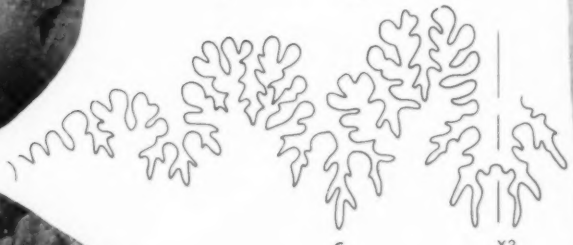

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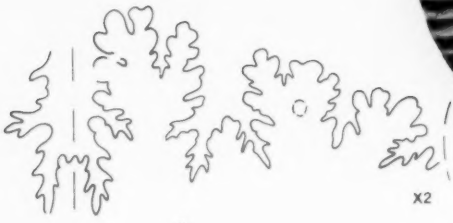

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feet below base of Gaikema member of Tuxedni formation.

20001 Helmuth Wedow, Jr., and L. B. Kellum 1944. Iniskin Peninsula, northeast side of Tonnie Creek 0.9 mile S 48° E of Tonnie Peak. Bowser member of Tuxedni formation, about 100 feet above base.

21258 R. W. Imlay and D. J. Miller, 1948. Same as Mes. Loc. 19773.

21282 R. W. Imlay and D. J. Miller, 1948. Tuxedni Bay area, on tributary entering Bear Creek from the southeast 4.75 miles S 22° W of Fossil Point. Bowser member of the Tuxedni formation, about 300 feet above base.

21313 R. W. Imlay and D. J. Miller, 1948. Iniskin Peninsula. Same as Mes. Loc. 11036.

21314 R. W. Imlay and D. J. Miller, 1948. Iniskin Peninsula. Same as Mes. Loc. 11034.

21315 R. W. Imlay and D. J. Miller, 1948. Iniskin Peninsula on Cliff Creek near Mes. loc. 21313. Bowser member of the Tuxedni formation, float from lower 175 feet.

21318 R. W. Imlay and D. J. Miller, 1948. Iniskin Peninsula on Tonnie Creek 1.0 to 1.05 miles S 51° E of Tonnie Peak, Bowser member of the Tuxedni formation, 50 to 125 feet above base.

22529 Arthur Grantz, 1950. Lake Hickerson area, 5.3 miles S 55° E of peak of Mt. Iliamna. Siltstone about 300 feet below base of Gaikema sandstone member of the Tuxedni formation.

22709 Arthur Grantz, 1951. Tuxedni Bay area, 0.3 mile above mouth of tributary entering Bear Creek from southeast at point 2.53 miles from Tuxedni channel. Bowser member of the Tuxedni formation, about 100 feet above base.

24113 Arthur Grants, Richard Hoare and R. W. Imlay, 1952. Talkeetna Mountains A-1 quad., from a landslide scar 1.63 miles north of mouth of Albert Creek. Lower part of Tuxedni formation equivalent.

24821 Arthur Grantz and L. F. Fay, 1953. Anchorage D-2 quad. on Sheep Creek. Lat. 61° 59′ 17″ N., Long. 147° 38′ 35″ W., Tuxedni formation equivalent, upper half.

26593 R. L. Detterman, 1957. Inisikin Peninsula on Cliff Creek near Mes loc. 21313. Bowser member of the Tuxedni formation, 200 feet above base.

27099 R. L. Detterman, 1958. Iniskin Peninsula on Tonnie Creek 0.81 mile N 55° W of Iniskin Bay Association No. 1 well. Bowser member of the Tuxedni formation, 75 to 100 feet above base.

27577 Western Gulf Oil Co., 1959. Talkeetna Mountains A-1 quad., near Crooked Creek south of Nelchina, Lat. 62° 02′ N., Long. 147° 18′ W. Tuxedni formation equivalent, lower part.

SYSTEMATIC DESCRIPTIONS

Family OPPELIIDAE Bonarelli, 1893

Genus OPPELIA Waagen, 1869

Subgenus LIROXYITES Imlay, n. subgen.

This subgenus resembles *Oxycerites* Rollier in its highly involute coiling, discoid shape, sharp venter, and presence of numerous auxiliary lobes in its suture line. It differs by its falcoid ribs being much broader and more closely spaced, by the presence of conspicuous falcoid striae, and by the ribs and striae persisting well onto the adult body chamber instead of fading. Other possible distinctions are the weak crenulations on the keel formed by the continuations of the ribs and the striae; the presence on some specimens of two raised spiral bands instead of a single median spiral band; and the development of eccentric coiling on the adult body chamber. The type species of *Liroxyites* is *Oppelia* (*Liroxyites*) *kellumi* Imlay, n. sp.

EXPLANATION OF PLATE 64

All figures natural size unless otherwise indicated

FIGS. *1–3*—*Dettermanites vigorosus* Imlay, n. sp. *1*, paratype USNM 130897a from USGS Mes. loc. 11036 showing septate whorls. *2,3*, holotype USNM 130895 from USGS Mes. loc. 21318. Suture line (×2) drawn at whorl height of 18.5 mm at adoral end of outer septate whorl.

4–10—*Parabigotites crassicostatus* Imlay, n. sp. *4*, paratype USNM 130914 from USGS Mes. loc. 22529. Suture line (×2) drawn at whorl height of 7.5 mm. *5,6*, paratype USNM 130912 from USGS Mes. loc. 19966.; *7*, paratype USNM 130916 from USGS Mes loc. 27577; *8–10*, holotype, USNM 130909 from USGS Mes. loc. 11352. Suture line (×2) drawn near adoral end of outer septate whorl. Body chamber is represented by 1¼ whorls but does not show the aperture.

OPPELIA (LIROXYITES) KELLUMI
Imlay, n. sp.
Pl. 63, fig. 5,7–9

?*Oppelia* (*Oxycerites*) ex. gr. *fallax* (Guéranger), Frebold, 1957, Canada Geol. Survey Mem. 287, p. 54–56, pl. 28, fig. 2 (not figs. 1a, b)

This species is represented by 50 specimens of which most retain some shelly material. The shell is a discoidal, highly involute compressed oxycone. The coiling becomes slightly eccentric on the body chamber. The lower parts of the flanks are subparallel, but the upper parts converge toward the venter. The venter is acute and bears a narrow *open* keel (Arkell, 1957, p. 291) that is generally slightly pinched at its base and, wherever the shell is preserved, is marked by faint continuation of the ribbing. The umbilicus is extremely small on the septate part of the shell but widens a little on the body chamber. The umbilical wall is low, vertical, and rounds rather abruptly into the flanks. The body chamber occupies half a whorl. The aperture terminates abruptly in a gentle, forwardly incline, falcoid curve.

The ornamentation consists of weak to moderately strong falcoid ribs, falcoid striae and faint, broad spiral bands. The falcoid ribs are low and nearly as broad as the interspaces. They are barely visible at a diameter of 22 mm. and gradually become higher and broader during growth except near the aperture of the adult where they weaken. They arise near the middle of the flanks as bundles of striae, become stronger ventrally, weaken considerably at the keel and are faintly indicated on the keel wherever the shell is preserved. On internal molds, however, the ribs end abruptly at the keel. They do not split into secondary ribs. The falcoid striae cover the entire surface of the shell parallel to the ribs but unlike the ribs are not visible on the internal molds. On some specimens a faint spiral band occurs at about two-fifths of the height of the whorl and another at three-fifths of the height of the whorl.

The suture line is finely frilled, has a longer ventral than lateral lobe, and has seven auxiliary lobes that diminish regularly toward the umbilical seam.

Most of the specimens are too imperfect for accurate measurements. However, the specimen shown on plate 63, figure 7 at a diameter of 62 mm. has a whorl height of 35 mm., a whorl thickness of 13 mm., and an umbilical width of 4 mm

This species bears broad falcoid ribbing closely similar to that of an ammonite from the Fernie group of Alberta, Canada described by Frebold (1957, p. 54–56, pl. 28, fig. 2) as *Oppelia* (*Oxycerites*) ex. gr. *fallax* (Guéranger) and it may be identical specifically. However, it differs from the European *Oppelia* (*Oxycerites*) *fallax* (Guéranger), as described by Arkell (1951, p. 56–60, pl. 5, figs. 1–3; pl. 8, figs. 11a,b; text-figs. 15,16) by having broader, lower, and more closely spaced falcoid ribs that persist onto the adult body chamber. The large smooth adults of the European species of *Oxycerites* contrast markedly with the ribbed adult whorls of *Oppelia* (*Liroxyites*) *kellumi* Imlay, n. sp. from Alaska.

The eccentric coiling of the Alaskan species contrasts also with the tight coiling of most species *Oxycerites*, but does occur on *Oxycerites knapheuticus* (Buckman) (1924, pl. 479) from the lower Bathonian of England and on *Oxycerites tilli* (Loczy) (1915, pl. 4, fig. 3) from the Callovian of Hungary.

The weak spiral bands on the Alaskan species are not nearly as well developed as the spiral grooves and ridges on *Strigoceras* (see Arkell, 1957, p. L272) and are not accompanied by fine furrows and ridges, or by a hollow keel, as in that genus.

This species is named in honor of Lewis B. Kellum of the University of Michigan who collected some of the type specimens.

Types: Holotype, USNM 130886; paratypes, USNM 130887, b, 130888, 130889a-c, 130890.

Occurrence: Lower part of the Bowser member of the Tuxedni formation, Iniskin Peninsula, at USGS Mes. locs. 11035, 11036, 19943, 20001, 21282, 21313, 21314, 21315, 21318, and 27099.

Family OTOITIDAE Mascke, 1907
Genus MEGASPHAEROCERAS, n. gen.

This genus resembles *Sphaeroceras* Bayle in its globular shape, tiny umbilicus, sharp, wiry ribbing, and a tendency for the internal mold to be smooth or nearly smooth. It differs markedly, however, by the adult body chamber remaining tightly coiled

except at the aperture enlarging adorally instead of contracting, and bearing much weaker ribbing than the septate whorls. Furthermore, the apertural constriction is followed by a weak swelling rather than by a flared collar and the adults are much larger than in any described species of *Sphaeroceras*. The suture line has moderately broad lobes and saddles, has an irregularly trifid first lateral lobe that is slightly longer than the ventral lobe, and bears a general resemblance to that of the genus *Labyrinthoceras* Buckman (1919, pls. 134,135).

The type species of *Megasphaeroceras* is *M. rotundum* Imlay, n. sp.

MEGASPHAEROCERAS ROTUNDUM
Imlay, n. sp.
Pl. 63, figs. 1–4,6

The species is represented by about 60 specimens. The shell is stout to moderately stout and is tightly coiled. The whorls are depressed, wider than high, widest on the lower fourth of the flanks, becoming more depressed with growth, embracing preceding whorls nearly completely. The flanks and venter are evenly convex. The umbilicus is extremely small. The umbilical wall is low, vertical at base, and rounds fairly abruptly into flanks. The body chamber is represented by three-fifths to three-fourths of a whorl. The aperture curves strongly forward and terminates abruptly. It is marked on the internal mold by a broad constriction followed by a weak swelling that is not apparent where the shell is preserved. At the apertural constriction there is a slight contraction of the body whorl.

The ribbing on the septate part of the shell is sharp and gently flexuous. The primary ribs are radial on the umbilical wall and curve forward on the lower fourth of the flank where some of them bifurcate. From 1 to 3 secondary ribs arise freely near the zone of furcation between the primary ribs. All secondary ribs become higher and sharper ventrally, curve forward on the flanks, and cross the venter with a slight forward arching.

The ribbing on the adult body chamber weakens considerably but persists adorally to near the aperture as low broad ribs and striae. The shell at the apertural constriction is marked only by striae.

The ribbing on the internal molds of the septate whorls is much weaker than on the shell, but the greatest weakening occurs on the internal molds of the adult body chamber where the ribbing becomes very weak and on some specimens is indistinct.

The suture line is rather finely divided and has moderately broad saddles and lobes. The first lateral lobe is irregularly trifid and slightly longer than the ventral lobe. The second lateral lobe is much shorter and narrower than the first. The second lateral saddle is broader and lower than the first lateral saddle. The general sutural pattern is similar to that of *Labyrinthoceras intricatum* Buckman (1919, pl. 135). The suture line of *Sphaeroceras brongniarti* (J. Sowerby) illustrated by Westermann (1956, text-fig. 6 on p. 31) has a broader first lateral lobe and a narrower second lateral saddle.

The dimensions of the type specimens in millimeters are as follows:

Specimen	Diameter	Whorl height	Whorl thickness
Paratype 130899c	92?	53	?
Holotype 130898	62	33	42?
Paratype 130899b	63	35	?
Paratype 130899d	48	30	34
Paratype 130899a	41	25	25

Types: holotype, USNM 130898; paratypes, USNM 130899a-d, 130900

Occurrence: Lower part of Bowser member of the Tuxedni formation at USGS Mes. locs. 11035, 11036, 19943, 21282, 21313, 21314, 21315, 21318, 22709, 26593.

Family STEPHANOCERATIDAE
Neumayr, 1875
Genus DETTERMANITES Imlay, n. gen.

This genus resembles *Stephanoceras* in coiling, shape, ornamentation and sutural pattern, but differs by having elongate lateral lappets. In this respect it is similar to *Polyplectites*, but differs by being much larger, by developing coarser ribbing on its body chamber, and by its ventral lobe being appreciably longer than its first lateral lobe. In *Polyplectites* these lobes as illustrated by Westermann (1954, p. 337,341,345) are nearly of the same length. The genus *Normannites*, whose long lateral lappets some-

what resemble those of *Dettermanites*, has fewer secondary ribs that are much stronger relative to the primary ribs. Both ribbing and sutural pattern indicate an assignment of *Dettermanites* to the Stephanoceratidae rather than to the Otoitidae.

The type species of *Dettermanites* is *D. vigorosus* Imlay, n. sp.

This genus is named in honor of Robert L. Detterman of the Alaskan Geology Branch of the U. S. Geological Survey.

DETTERMANITES VIGOROSUS
Imlay, n. sp.
Pl. 64, figs. 1–3

This species is represented by 10 specimens preserved in concretions that with 3 exceptions reveal only one side of the specimen. The whorls are nearly coronate in section, much wider than high, and embrace the preceding whorls nearly one-half. The body whorl is slightly contracted from the penultimate whorl. The umbilicus is moderately wide. Its wall is steeply inclined and rounds evenly into the flanks. The body chamber occupies about three-fourths of a whorl. The aperture bears lateral lappets. It is marked on internal molds by a constriction, followed by a collar, and then by lappets.

The ribbing consists of prominent widely-spaced primary ribs that incline forward slightly and terminate near the middle of the flanks in acute tubercles. From these pass bundles of two, or rarely three, much weaker secondary ribs that incline forward on the flanks and cross the venter transversely. Many rib bundles are separated by single ribs that arise freely along the zone of furcation. Both ribs and tubercles become gradually stronger and sparser during growth.

The suture line is characterized by its ventral lobe being appreciably longer than the first lateral lobe and by the second lateral lobe being much shorter. The first first lateral lobe is irregularly trifid.

The holotype at a diameter of 89 mm., has a whorl height of 32 mm., an estimated whorl thickness of 36 mm., and an umbilical width of 41 mm.

This species has much coarser ribbing than any described species of *Polyplectites* except possibly *P. dorni* (Roche) (1939, p. 222; Dorn, 1927, p. 240, pl. 5, fig. 6; Westermann, 1956, p. 342, pl. 32, figs. 4a,b) which is much smaller and apparently less evolute.

Types: holotype, USNM 130895; paratypes, USNM 130896, 130897a,b.

Occurrence: Lower part of Bowser member of the Tuxedni formation, Iniskin Peninsula, at U.S.G.S. Mes. locs. 11034–11036, 19934, 21314 and 21318. Talkeetna Mountains at U.S.G.S. Mes. locs. 8572 and 24821.

Family PERISPHINCTIDAE
Steinmann, 1890
Subfamily LEPTOSPHINCTINAE
Arkell, 1950
Genus PARABIGOTITES, n. gen.

This genus is characterized by highly evolute coiling; by ovate depressed whorl sections; by high, sharp, forwardly inclined ribs that bifurcate above the middle of the flanks and are not interrupted on the venter; by the ribbing remaining strong on the body chamber; by the peristome terminating simply, and by the suspensive lobe being strongly retracted.

It greatly resembles *Bigotites* Nicolesco (1918, p. 36) in shape, coiling, and ribbing. It differs by lacking a smooth band along the midventral line, by the secondary ribs merely arching forward gently on the venter instead of forming an obtuse angle, by its constrictions being less strongly developed, and by having a strongly retracted suspensive lobe. Furthermore its constrictions are not followed by segmental enlargements of the shell or by changes in the ribbing such as described by Nicolesco (1931, p. 9–12) for *Bigotites*.

Parabigotites shows great resemblances, also, to *Prorsisphinctes* Buckman (1921, pl. 200; Siemeradzki, 1899, pl. 22, fig. 27) which Arkell (1957, L314) considers to be a subgenus of *Leptosphinctes*. It differs by having sharper, higher ribbing that becomes stronger adorally on the adult whorls instead of weakening or fading. It appears also to be more evolute and to have a lower whorl section.

The type species of *Parabigotites* is *P. crassicostatus* Imlay, n. sp.

PARABIGOTITES CRASSICOSTATUS
Imlay, n. sp.
Pl. 64, figs. 4–10

Dactylioceras sp. A. 1945, Kellum, Daviess and Swinney, U. S. Geol Survey, figs. 5A-B (not C-E)

This species is represented by about 65 specimens of various sizes of which most are crushed and fragmentary. The shell is discoidal and moderately compressed. The whorls are ovate in section, a little wider than high, and embrace about one-fourth of the preceding whorls. The flanks and venter are evenly rounded. The umbilicus is wide and shallow. The umbilical wall is low, nearly vertical, and rounds evenly into the flanks. The incomplete body chamber on the holotype is represented by four-fifths of a whorl. The apertural margin is simple, is projected forward slightly on the venter, and is preceded by a nearly smooth area.

The small and intermediate sized whorls bear prominent, widely spaced primary ribs that incline forward gently on the lower parts of the flanks and pass abruptly into weaker secondary ribs at about two-fifths of the height of the flanks. The ventral ends of the primary ribs are strongly swollen but are not distinctly tuberculate. The secondary ribs arise in pairs that incline forward on the flanks more strongly than the primary ribs. All secondary ribs arch forward gently on the venter which they cross without interruption. Two or three weak constrictions occur on each whorl.

Adorally on the penultimate and body whorls the ribbing becomes increasingly coarser, the secondary ribs become nearly as strong as the primary ribs and the constrictions become more pronounced. Many of the secondary ribs are indistinctly connected with the primary ribs and some arise freely along the zone of furcation. All secondary ribs arch forward on the venter which they cross without weakening.

The suture line, partly exposed on the holotype, is characterized by broad saddles, by the second lateral saddle being almost as wide and high as the first lateral saddle, and by the suspensive lobe being well retracted.

The holotype has been crushed somewhat laterally, but at a diameter of 102 mm., has a whorl height of 28 mm., a whorl thickness of 32 mm., and an umbilical width of 54 mm. On paratype USNM 130910, the same dimensions are 83, 20, 23, and 46 mm. respectively.

The appearance of this species in lateral view is strikingly similar to that *Bigotites pulcher* Nicolesco (1931, p. 21, pl. 2, fig. 1) from Europe, differing mainly in its somewhat higher, sharper, and more closely spaced ribs, and less pronounced constrictions. In ventral view it is readily differentiated, however, by lacking a smooth midventral area and by the ribs arching evenly across the venter instead of meeting at an angle along the midventral line. It differs from most of the species of *Leptosphinctes* (*Prorsisphinctes*) (Buckman, 1921, pls. 200, 211,247; 1922, p. 326; 1923, pl. 386,446; 1925, pls. 544,545) by having much coarser ribbing that becomes stronger on the body chamber instead of becoming weaker. However, its inner whorls are similar in appearance to the small specimen described as *Phanerosphinctes phanerus* Buckman (1921, pl. 211), which Arkell (1958, p. 168) assigns questionably to *Prorsisphinctes*

Type: Holotype, USNM 130909; paratypes, USNM 130910–130916.

Occurrence: Kialagvik formation at USGS Mes. locs. 11352, 12404, 19773, 19796, 19800, 19811, 19824, 21258 in the Alaska Peninsula; lower siltstone member of the Tuxedni formation at USGS Mes. locs. 19966, 22529, 25831 on the north side of Cook Inlet; Tuxedni formation equivalent at USGS Mes. loc. 24113 in the Talkeetna Mountains.

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ORBITOLINAS FROM CARIBBEAN ISLANDS[1]

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ABSTRACT—The foraminiferal genus *Orbitolina* is recognized in the Dominican Republic, Puerto Rico, Barbados, and Trinidad. The species present indicate an Albian (Early Cretaceous) age. *Orbitolinoides senni* Vaughan is recognized as a species of *Orbitolina*.

INTRODUCTION

Orbitolina-bearing limestone samples from four islands in the Caribbean area present an interesting extension of a study on the orbitolinas of North America (Douglass 1960). Three of the occurrences under consideration have been noted previously. *Orbitolina* sp. was mentioned and illustrated by Vaughan and Cole (1941, p. 31, pl. 8, figs. 2,3,4) from Trinidad. Specimens of *Orbitolina* were illustrated and described as *Orbitolinoides senni* by Vaughan (1945, p. 22, pl. 2) from Barbados, and *Orbitolina concava texana* was mentioned from the Dominican Republic by Woodring (1954, p. 723). The fourth occurrence is from Puerto Rico and was recognized in material submitted for examination by James P. Owens.

None of the samples available is large and in the material from Trinidad, the originally figured specimens are all that are available for study. The material from the Dominican Republic was provided by W. P. Woodring. MacGillavry (1937, p. 11), Maync (1949, p. 532) and Woodring (1954, p. 723) have mentioned *Orbitolina* from the Cretaceous of Cuba but no specimens are available for comparison in this study.

DOMINICAN REPUBLIC

Two samples of *Orbitolina* in limestone are available from the Dominican Republic (localities 1 and 2, text-fig. 1):

1. Collection W-18 of W. P. Woodring, Dec. 24, 1941, on the road from Hato Mayor to Sabana de la Mar, 8 kilometers north-north-west of Hato Mayor, Seibo Province, Dominican Republic.
2. Collection W-19 of W. P. Woodring, Dec. 24, 1941, on the road from Hato Mayor to Sabana de la Mar, 9.2 kilometers north-north-west of Hato Mayor, Seibo Province, Dominican Republic.

Thin sections were prepared from selected random slices of the limestone of each sample. The specimens in collection W-18 are illustrated on plate 65 as figures 6,8–15. They are assignable to *Orbitolina oculata* Douglass. In North America this species is found in the upper part of the Glen Rose limestone equivalents in Arizona and New Mexico. In the Caribbean it is also found in Puerto Rico and Trinidad. It has well developed marginal and radial zones and has common to abundant calcite eyes in the central complex.

The specimens in collection W-19 are illustrated on plate 66 as figures 1–4. They are assignable to *Orbitolina minuta* Douglass. This species is common throughout the upper part of the Glen Rose limestone and

TEXT-FIG. 1—Localities 1 and 2 in the Dominican Republic.

[1] Publication authorized by the Director, U. S. Geological Survey.

its equivalents in North America from Arizona to Florida. In the Caribbean this species has not been recognized on the other islands. It has well developed marginal and radial zones and no calcite eyes.

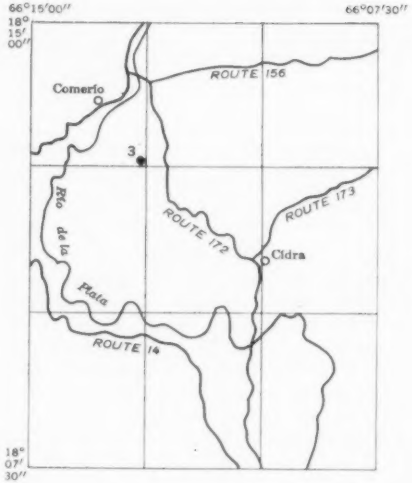
Woodring (1954, p. 722–23) mentioned the occurrence of *Orbitolina concava texana* in limestones of the Cordillera Central of the Dominican Republic. He considered them to be of Aptian-Albian age. The Albian age appears to be the more likely, based on the orbitolinas.

PUERTO RICO

During a program of mapping in Puerto Rico samples of limestone were sent to the author for study of the micro-faunas. Two samples collected by J. P. Owens contained specimens of *Orbitolina*. They are:

3. Collection JP0-CE-2 of James P. Owens from the point shown on text-figure 2 southeast of Comerio, Comerio quadrangle, Puerto Rico.
4. Collection JP0-CY-1 of James P. Owens from the point shown on text-figure 3 southwest of Cayey, Cayey quadrangle, Puerto Rico.

The specimens from JP0-CE-2 are illustrated on plate 65 as figures 4,5,7 and are assignable to *Orbitolina oculata* Douglass. Although the specimens from JP0-CY-1 are poorly preserved and not illustrated, they are also assignable to *Orbitolina oculata* Douglass.



TEXT-FIG. 2—Locality 3 in the Comerio quadrangle Puerto Rico.

BARBADOS

One or more free specimens of *Orbitolina* are available from each of the following localities (shown on text-fig. 4):

5. Barbados. St. Andrew's Parish. Mur

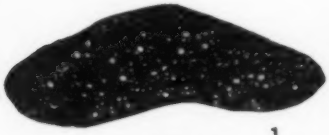
EXPLANATION OF PLATE 65

Magnifications ×10 except figs. 11 and 15, which are ×20

FIGS. *1–3—Orbitolina oculata* Douglass from Trinidad. *1.* Subaxial section, USNM 545833; *2.* Deep tangential section, USNM 545834; *3.* Subaxial section, USNM 545835. All from H. G. Kugler K2945d.

4,5,7—Orbitolina oculata Douglass from Puerto Rico. ×10. *4.* Subaxial section, USNM 627401; *5.* Subaxial section, USNM 627402; *7.* Basal section, USNM 627403. All from J. P. Owens CE-2.

6,8–15—Orbitolina oculata Douglass from the Dominican Republic. *6.* Subaxial section, USNM 627404; *8.* Oblique section, USNM 627405; *9.* Basal section, USNM 627406; *10.* Oblique section, USNM 627407; *11.* Partial axial section just grazing the proloculus, USNM 627408; *12.* Oblique section, USNM 627409; *13.* Oblique section, USNM 627410; *14.* Basal section, USNM 627411; *15.* Basal section, USNM 627412; All specimens from W. P. Woodring W-18.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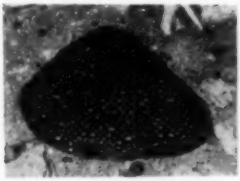
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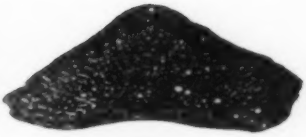
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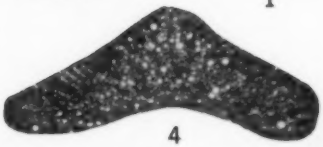
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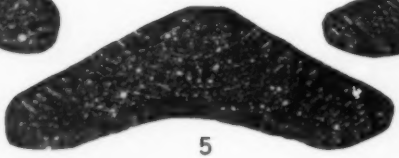
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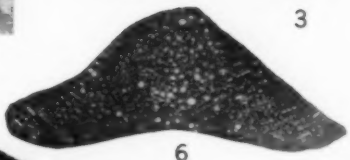
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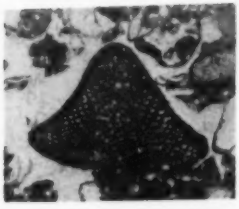
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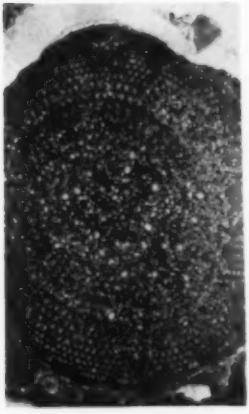
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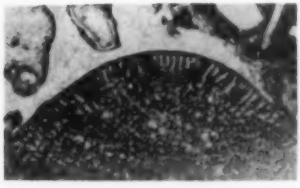
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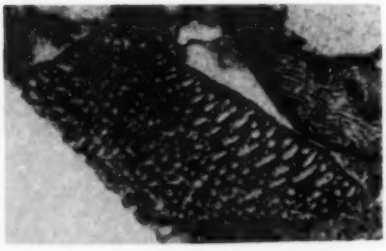
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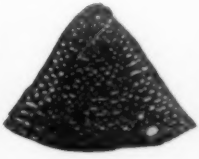
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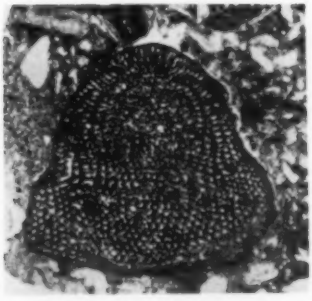
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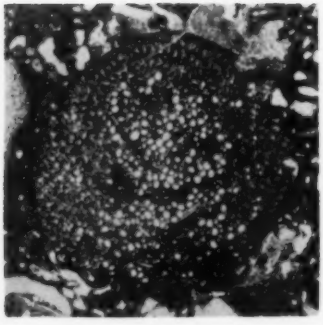
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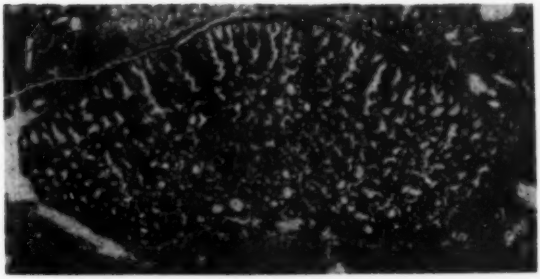
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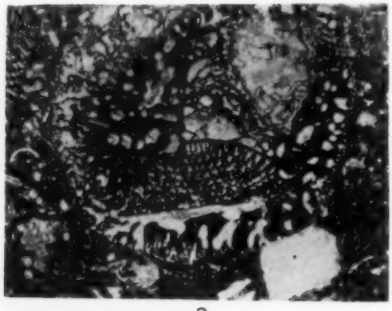

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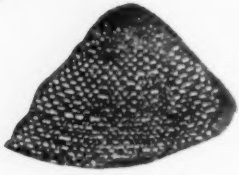

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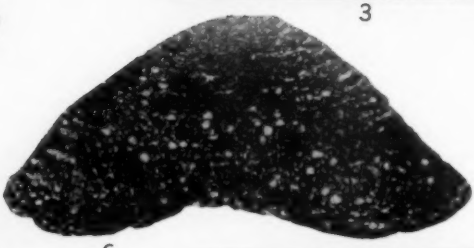

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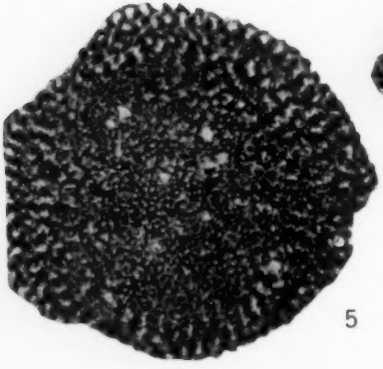

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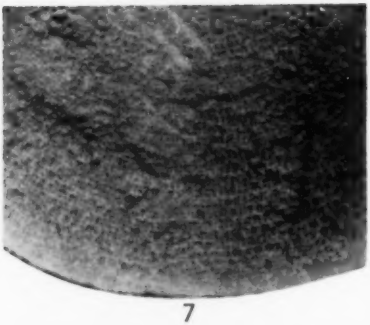

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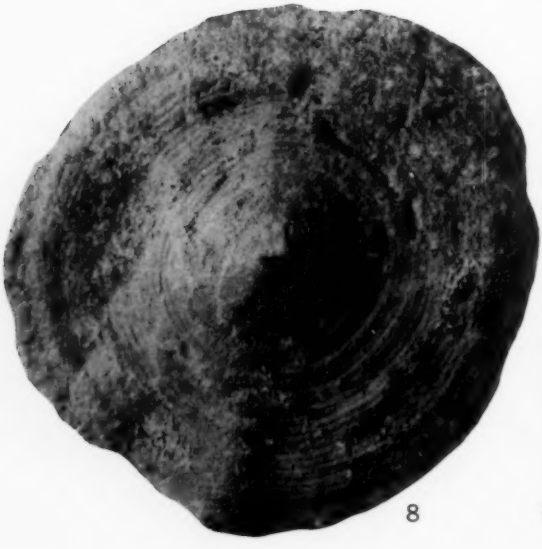

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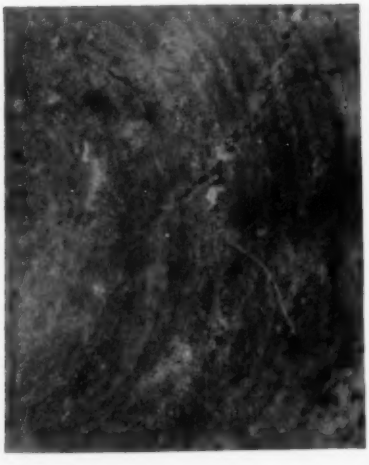

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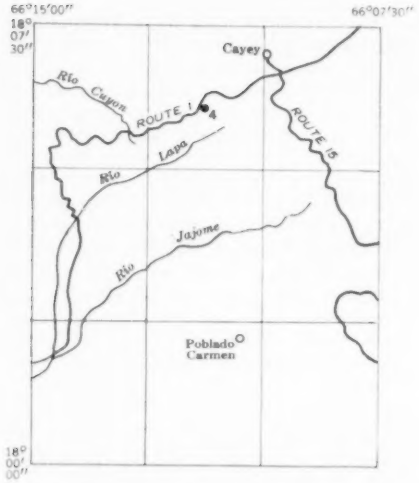
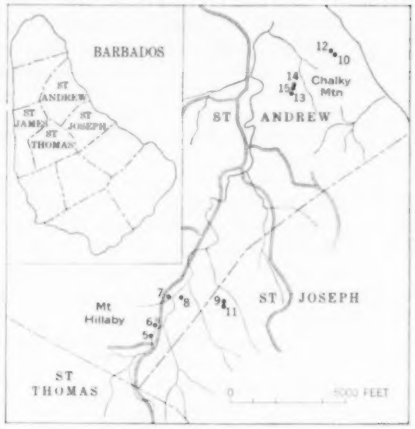


TEXT-FIG. 3—Locality 4 in the Cayey quadrangle, Puerto Rico.



TEXT-FIG. 4—Outline map of Barbados, and map of the Scotland district with localities 5 to 15.

phys member of the Upper Scotland formation on left bank of Murphys River, west of Murphys village, 2–3 meters southwest of confluence with Groves River. Collection S. 34C. of A. Senn, Aug. 18, 1937.

6. Barbados. St. Andrew's Parish. Chalky Mount member of Upper Scotland formation on ridge on northern side of Murphys River, 65 meters northwest of Murphys Bridge. Collection S. 36 of A. Senn, July 26, 1937.
7. Barbados. St. Andrew's Parish. Middle Chalky Mount member of Upper Scotland formation in left bank of Mount Hillaby River 46–54 meters east of Murphys-Friendship road. Collection S. 58 of A Senn. August 20, 1937.
8. Barbados. St. Andrew's Parish. Base of lower Chalky Mount member of Upper Scotland formation on small road leading from Friendship-Estate to Mahogany Wood on Richmond Ridge, in curve about 100 meters east of Friendship Bridge on Murphys River. Collection S. 61 of A. Senn. August 21, 1937.

EXPLANATION OF PLATE 66

Magnifications ×10 except figs. 6, 7, and 9, which are ×20

FIGS. *1–4*—*Orbitolina minuta* Douglass from the Dominican Republic. *1*. Strongly oblique section, USNM 627413; *2*. Oblique section, USNM 627414; *3*. Oblique section enclosed by algae, USNM 627415; *4*. Deep tangential section, USNM 627416. All specimens from W. P. Woodring W-19.

5–9—*Orbitolina senni* (Vaughan) from Barbados. *5*. Basal section of a cotype from S102A figured by Vaughan (1945, pl. 2, fig. 4), USNM 627417; *6*. Subaxial section of a cotype from S168 figured by Vaughan (1945, pl. 2, fig. 5), USNM 627418; *7*. portion of the surface of a specimen from S36 showing the subdivisions of the marginal zone, USNM 627419; *8*. Upper surface of a cotype from S58 figured by Vaughan (1945, pl. 2, fig. 2), USNM 627420; *9*. Portion of the upper surface of the same specimen ×20 to show the subdivisions of the marginal zone.

9. Barbados. St. Joseph's Parish. Base of middle Chalky Mount member of Upper Scotland formation in slope between Spa Peak Canegarden River on western side of cross-fault scarp. Collection S. 80 of A. Senn. Sept. 13, 1957.
10. Barbados. St. Andrew's Parish. Chalky Mount member of Upper Scotland formation in northern slope of Chalky Mount. Collection S. 102 of A. J. Mestier and A. Senn. March 1, 1938.
11. Barbados. St. Joseph's Parish. Top of lower Chalky Mount member of Upper Scotland formation along footpath on northeastern side of Spa Peak. Collection S. 152 of A. J. Mestier, J. Rose, and A. Senn. July 10, 1938.
12. Barbados. St. Andrew's Parish. Upper Chalky Mount member of Upper Scotland formation on northern slope of Chalky Mount near Senn locality S. 102 (Loc. 10 above). Collection S. 168 of A Senn. Oct 22, 1938.
13. Barbados. St. Andrew's Parish. Middle Chalky Mount member of Upper Scotland formation in western part of Chalky Mount massif, at northeastern side of flat-topped ridge 80–90 meters south of S. 375 (loc. 15 below) and 165–180 meters SSW. of S. 360 (loc. 14 below) Collection S. 359 of A. Senn. Sept. 28, 1942.
14. Barbados. St. Andrew's Parish. Middle Chalky Mount member (upper part) of Upper Scotland formation on prominent ridge in western part of Chalky Mount massif (approximately 550 meters WSW. of highest summit of Chalky Mount. Collection S. 360 of A. Senn, May 16, 1939. A. S. Mestier June 6, 1939.
15. Barbados. St. Andrew's Parish. Middle Chalky Mount member (upper part, same horizon as S. 360 or loc. 14 above) of Upper Scotland formation in western part of Chalky Mount massif, in small ravine approximately 100 meters southwest of S. 360 (loc. 14 above). Collection S. 375 of A. Senn. June 6, 1939 and November 5, 1940.

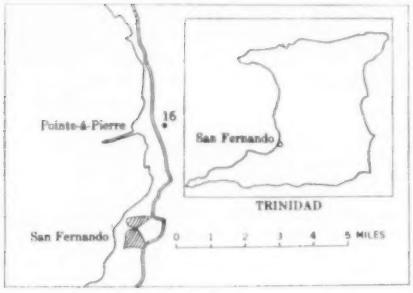
The specimens from these samples were described by Vaughan (1945, p. 23, pl. 2) as *Orbitolinoides senni* Vaughan, n. gen. n. sp. He distinguished between these and *Orbitolina* on the basis of the supposed absence of a marginal zone in the Barbadian specimens. Study of the types reveals a thin but well developed marginal zone on these specimens. Many of the specimens are abraded and the marginal zone is partly or completely removed, but two of the illustrated cotypes and two paratypes have the marginal zone preserved. Plate 66 figures 5,6,8,9 illustrate three of the originally figured cotypes. *O. senni* is an *Orbitolina*. Plate 66, figure 7 is a previously unfigured paratype with the surface just slightly eroded and showing the cellular subdivisions of the marginal zone. *Orbitolina senni* (Vaughan) resembles *Orbitolina oculata* Douglass in some respects but is sufficiently different in the development of the marginal and radial zones to be recognized as a distinct species. Most of the specimens available have been described in tabular form by Vaughan (1945, p. 24, table 1).

The age of the Barbadian material is problematic. The specimens of *Orbitolina* appear to represent an Early Cretaceous (Albian) age. The collections to which they are attributed, however, are reported to be of Eocene age (Vaughan, 1745, p. 4,5). Vaughan noted, however, that blocks of pre-Eocene rock have been incorporated in the Scotland formation by mud-flows and it is possible that the orbitolinas were introduced from such blocks. Although many of the specimens are worn, there is no direct evidence of their being reworked and no known rocks of Cretaceous age outcrop on the island.

TRINIDAD

Three thin-sections of a limestone containing orbitolinas from Trinidad are present in the U. S. National Museum foraminifera collections. They are from Collection K2945d of H. G. Kugler from a block in a boulder bed on the Bon Accord Estate, Pointe-a-Pierre, Trinidad. Lat. N. 10°19′20″ Long. W. 61°27′10″. This locality is plotted as No. 16 on text-figure 5.

Three random sections of *Orbitolina ocu-*



TEXT-FIG. 5—Locality 16 near Pointe-a-Pierre, Trinidad.

lata Douglass are represented and are illustrated on plate 1 as figures 1–3. Vaughan and Cole (1941, p. 31, pl. 8, figs. 2–4) noted the specimens and referred them to *Orbitolina* sp., stating that they were probably referrable to *O. texana* (Roemer).

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MANUSCRIPT RECEIVED JANUARY 20, 1960

JOURNAL OF PALEONTOLOGY, V. 35, NO. 3, P. 480–488, PLS. 67–68, 2 TEXT-FIGS., MAY, 1961

MIOCENE ECHINOIDS FROM THE VALLE CENTRAL, COSTA RICA*

J. WYATT DURHAM†

ABSTRACT—*Echinolampas woodringi* n. sp., *Pericosmus israelskyi* n. sp., *Schizaster costaricensis* n. sp., *Schizobrissus kewi* n. sp., *Plagiobrissus costaricensis* n. sp., and *P. malavassii* n. sp. are described. *Brissopsis* n. sp., and *Clypeaster* sp. indet. are recorded and figured. It is concluded that the echinoids probably lived in water between 100 and 300 meters deep. Most of these echinoids have their closest relatives in the Mesón and Tuxpan formations of Mexico and the Ojo de Agua formation of Venezuela.

THE echinoids described here were collected by Enrique Malavassi V. from the east slope of the ridge between Candelaria triangulation station and Río Ciruelas, 2.9 km. south-southeast of Turrúcares, San José Province, Costa Rica (USGS locality 20001) in 1957. They were subsequently submitted to me for identification and description by W. P. Woodring, of the United States Geological Survey. I am grateful to Dr. Woodring and Señor Malavassi for the opportunity of studying them. Reference should be made to the accompanying paper by Woodring and Malavassi for an account of the stratigraphy at the fossil locality and conclusions as to the age. The Committee on Research of the University of California supplied funds for preparation of the illustrations.

The specimens from this locality are assigned to eight species representing seven genera. Seven of the species are considered to be new, although one (*Brissopsis* n. sp.) is not named because the single specimen is too incomplete. The eighth species (*Clypeaster* sp. indet.) is represented by two incomplete specimens that are inadequate for specific comparison. *Schizaster costaricensis* n. sp. is by far the most abundant species, being represented by 10 specimens. *Pericosmus woodringi* n. sp. is represented by three individuals, the other species by one or two specimens only.

Ecology.—*Schizaster orbignyanus* A. Agassiz, which is the living species most closely related to *S. costaricensis* n. sp. is recorded (Mortensen, 1951, p. 306–308) from depths of 120–365 meters. The other living species of the genus mostly occur in shallower water. Seven of the nine known living species of *Pericosmus* (Mortensen, 1951, p. 176–200) are recorded from depths of 90 to 486 meters, one species was dredged from a depth of 18 to 70 meters, and the depth range for the ninth species is unknown. Species of the genus *Plagiobrissus*, represented in the collection by three specimens, are found living (Mortensen, 1951, p. 496–500) mostly in "shallow water." The genus *Echinolampas* had its major development in the Early Tertiary, but is represented by at least three living species that are found in depths (Mortensen, 1948, p. 267–268) of eight to 1600 meters. The numerous living species of *Brissopsis* (Mortensen, 1951, p. 380–432) occur in shallow water and out to depths of over 2000 meters. The genus *Clypeaster* is largely littoral to sublittoral in habitat, but it is known to occur at depths as great as 500 meters (Durham, 1955, p. 121). The genus *Schizobrissus* is extinct. Summarizing the above data on the bathymetric range of the living relatives of the members of this fauna, it seems most probable that the fossils lived in waters between 100 and 300 meters deep.

Age.—The genus *Schizobrissus* is recorded from the Eocene through the Miocene (Mortensen, 1951, p. 454). *S. kewi* n. sp. most closely resembles *Macropneustes dubius* Israelsky (1924) from the Tuxpan formation of the Tampico, Mexico area. The Tuxpan formation is currently assigned to the lower Miocene (Vindobonian and latest Burdigalian) in the terminology of the guidebook for the Tampico embayment prepared for the XX International Geological Congress (Maldonado Koerdell, 1956, p. 16, 87–90). *Schizaster dumblei* Israelsky, a close relative

* A contribution from the Museum of Paleontology of the University of California.

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of *S. costaricensis* n. sp., was described from Dumble's San Rafael beds (now referred to the Mesón formation, see Muir, 1936, p. 133), and also occurs in the Tuxpan formation (Maldonado Koerdell, 1956, p. 88). The Mesón formation was assigned to the upper Oligocene and correlated with the European late Chattian and Aquitanian in the guidebook referred to above (Maldonado Koerdell, 1956, p. 16, 71–76). It is to be noted that in this guidebook the Aquitanian is considered to be upper Oligocene rather than lower Miocene as is common usage in most current American works (*e.g.* Cooke, Gardner, and Woodring, 1943). Thus on the basis of the guidebook age assignments, the Mesón and Tuxpan formations would be referred to the lower and middle Miocene, respectively, in the usual North American terminology. *Schizaster costaricensis* n. sp., however, seems to be most closely related to the *S.* cf. *eurynotus* of Jeannet (1928) from the Ojo de Aqua formation of Venezuela. This formation has been assigned to the upper Miocene and correlated with the European Sarmatian and Pontian by Renz (1948, p. 77). *Echinolampas woodringi* n. sp. is related (but not closely) to *E. aldrichi* Twitchell from the late Oligocene Chickasawhay formation of the Gulf Coast. *Pericosmus israelskyi* n. sp. is comparable to *P. stehlini* Jeannet from the Caujarao formation ("Damsite series") of Venezuela, of lower middle Miocene (correlated with the European late Burdigalian and Helvetian by Renz, 1948, p. 77) age. *Plagiobrissus malavassii* n. sp. seems to be closely related to the fragmentary *P. lamberti* Jeannet from the lower Ojo de Agua formation of Venezuela. The three other species in the collection do not furnish a basis for any significant comparison. In summary, the new echinoids from Costa Rica are most closely related to species that are recorded from formations of lower, middle and upper Miocene (in common American usage) ages.

SYSTEMATIC DESCRIPTIONS

Genus ECHINOLAMPAS Gray, 1825

Type species ECHINANTHUS OVATUS Leske

ECHINOLAMPAS WOODRINGI n. sp.

Pl. 68, figs. 2,3,7; text-fig. 1,A; text-fig. 2,A.

Test of medium size, periproct and peristome only partially preserved; outline nearly rounded; test slightly depressed, with apical system rising to slight point; apical system about three-sevenths distance from anterior end; petals slender, pores in outer row only slightly longer than in inner row; in paired petals posterior row of pore-pairs considerably longer than anterior row; ambitus rounded; peristome slightly anterior, floscelle poorly developed; peristome elongated laterally; periproct moderately large, ovate, submarginal.

Dimensions of holotype: length 61.4 mm., width about 59.5 mm., height 28.3 mm.

Types: holotype, U. S. Nat. Mus. no. 563454; 2 paratypes, U. S. Nat. Mus. nos. 563455.

This species is related to *Echinolampas aldrichi* Twitchell from the late Oligocene Chickasawhay marl of Alabama and Mississippi, but differs from it by having a less elevated apical system and more inflated margins, as well as by more slender petals.

Genus CLYPEASTER Lamarck, 1801

Type species: CLYPEASTER ROSACEUS Lamarck = ECHINUS ROSACEUS Linnaeus

CLYPEASTER sp. indet.

Pl. 68, fig. 4.

Two fragments of an unidentifiable flattened *Clypeaster* with an inflated margin, elongate raised petals and moderately elevated petaloid area. In general aspect the fragments suggest the living *C. ravenellii* (A. Agassiz) but the elevated and nearly closed petals readily distinguish the fossil. The best specimen was probably about 90 mm. long.

Hypotypes, U. S. Nat. Mus. nos. 563456, 563457.

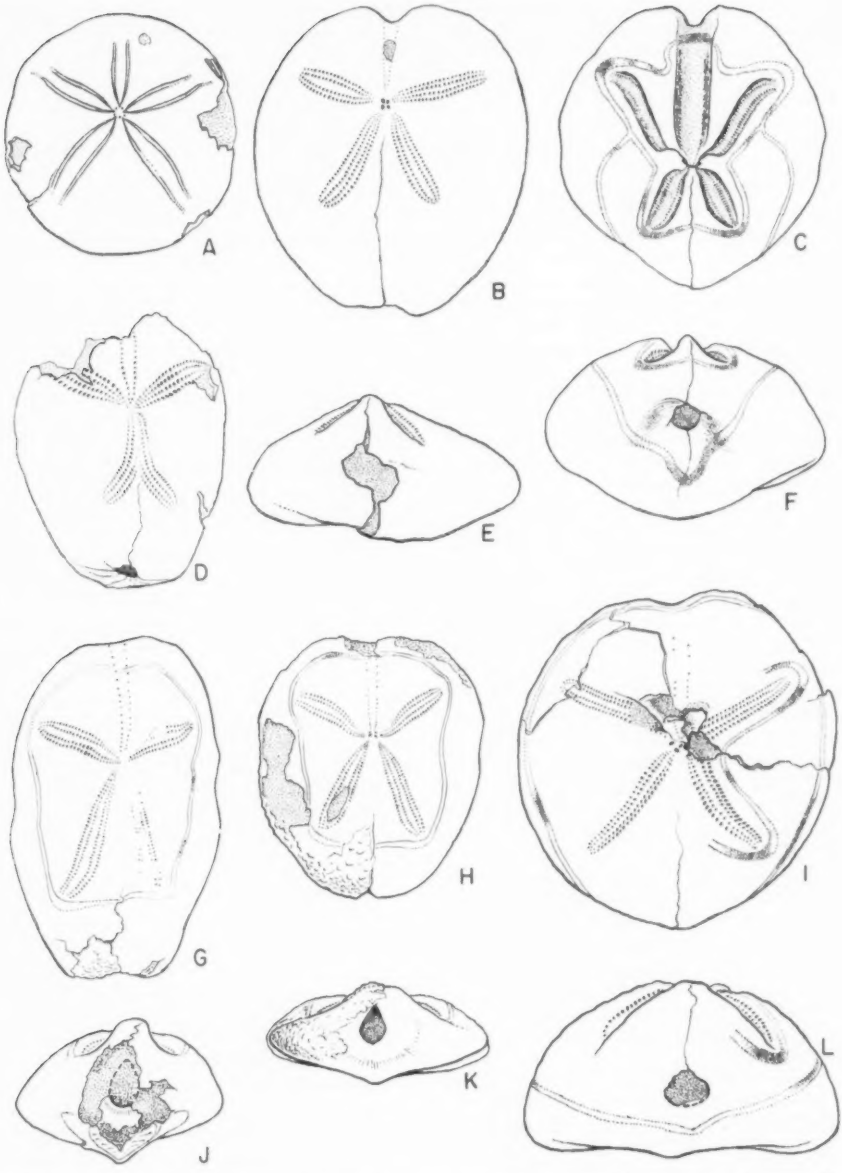
Genus PERICOSMUS L. Agassiz, 1847

Type species PERICOSMUS LATUS L. Agassiz.

PERICOSMUS ISRAELSKYI n. sp.

Pl. 67, figs. 5,8,11; text-fig. 1, I, L; text-fig. 2,E.

Test moderately large, hemispherical; apical system slightly anterior; paired petals long, well developed, rather deeply sunken; anterior petal in shallow depression; apical system crushed; surface eroded so that fascioles are indistinct; a slight aboral elevation in posterior interambulacrum with



TEXT-FIG. 1—All magnifications ×.67. The fascioles are well preserved in the stippled areas; the solid lines indicate traces present; dashed lines represent inferred position. *A.-Echinolampas wood-*

peristome about one-fourth distance from anterior margin; labrum short.

Dimensions of holotype: length 87 mm., width 83.8 mm., height 47.8 mm.

Holotype: U. S. Nat. Mus. no. 563458.

Among the species described from the New World, *Pericosmus israelskyi* appears to be most closely related to *Pericosmus stehlini* Jeannet (1928, p. 43–44, pl. 4, figs. 21–24) from the "Damsite Series (?)" of Venezuela, considered to be "middle Miocene (?)" by Jeannet. The "Damsite Series" is now termed the Caujarao formation and is referred to the lower middle Miocene by Renz (1948, p. 77). However *P. israelskyi* is higher proportionally and has a more rounded profile than Jeannet's species. Sanchez Roig (1949, p. 245–248, pl. 38, figs. 1–4) has recorded 3 species of *Pericosmus* (*P. roigi* Lambert, *P. camagüeyanus* Sanchez Roig, and *P. cubanus* Palmer in Sanchez Roig) from the Eocene and Oligocene of Cuba. His illustrations are not adequate for recognition of his species but from the measurements they are all more flattened than the Costa Rican species.

Genus SCHIZASTER L. Agassiz, 1836
Type species: S. STUDERI L. Agassiz

SCHIZASTER COSTARICENSIS n. sp.
Pl. 68, figs. 8,10,11,13; text-fig. 1,C,F; text-fig. 2,G,H.

Test moderately large, outline cordate; high posteriorly, sloping anteriorly; apical system about one-third distance from posterior end, petals strongly depressed; genital pores 2; posterior end truncated, overhanging, periproct high on truncation; interambulacrum 5 with strongly developed keel on apical surface; peristome slightly less than one-fifth distance from anterior end, labrum well developed; anterior paired petals nearly twice as long as posterior petals; anterior petal deeply excavate, broad, pore-pairs arranged in a single series, peripetalous and lateroanalfa scioles present; peripetalous fasciole closely paralleling outer edge of paired petals; adoral areas covered with large tubercles, tubercles on aboral surface much finer.

Dimensions of holotype: length 76.5 mm., width 70.7 mm., height 47.3 mm.

Types: Holotype, U. S. Nat. Mus. no. 563459; figured paratype, U. S. Nat. Mus. no. 563460; 8 other paratypes, U. S. Nat. Mus. no. 563461.

There are ten specimens of this species, all at least slightly distorted by crushing.

In all specimens the position of the apical system and relative lengths of the petals is about the same. In one poorly preserved specimen the width seems to be as great as the length, but in the others the relative dimensions are similar to those of the type.

This species belongs to the group of *Schizaster eurynotus* L. Agassiz, the type of *Aplospatangus* Lambert, 1907. Mortensen (1951, p. 300) considers *Aplospatangus* to be a true *Schizaster*, a conclusion which is here accepted.

This species is most closely related to *S.* cf. *eurynotus* Agassiz of Jeannet (1928, pl. V, figs. 6–8) but differs from it by being more elongate and having the posterior petals proportionally longer. *S. eurynotus* of the same author (*ibid.*, p. 44–47, pl. IV, figs. 25,26) has about the same proportions as the present species, but has shorter posterior petals. These two species are from the Ojo de Agua formation, considered by Jeannet to be of middle Miocene age but Renz (1948, p. 77, table 15) has referred this formation to the upper Miocene.

The living Caribbean *S. orbignyanus* A. Agassiz has a more central apical system and much shorter posterior petals than the present species, but seems to be the most closely related living species. *S. scherzeri* Gabb (1881, p. 348, pl. 45, figs. 28,28a,28b)

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ringi n. sp. Holotype, U. S. Nat. Mus. no. 563454. Apical view; B, E.-*Schizobrissus kewi* n. sp. Holotype, U. S. Nat. Mus. no. 563463. *B*, apical view. *E*, posterior view; *C*, *F.-Schizaster costaricensis* n. sp. Holotype, U. S. Nat. Mus. no. 563459. *C*, apical view. *F*, posterior view; *D.-Brissopsis* n. sp. Hypotype, U. S. Nat. Mus. no. 563462. Apical view; *G*, *J.-Plagiobrissus costaricensis* n. sp. Holotype, U. S. Nat. Mus. no. 563464. *G*, apical view. *J*, posterior view; *H*, *K.-Plagiobrissus malavassii* n. sp. Holotype, U. S. Nat. Mus. no. 563465. *H*, apical view. *K*, posterior view; *I*, *L.-Pericosmus israelskyi* n. sp. Holotype, U. S. Nat. Mus. no. 563458. *I*, apical view, *L*, posterior view.

from the Miocene "above Paquare, on the Reventazon river" of Costa Rica, is another related species. According to Gabb's figures his species has a more nearly central apical system and lacks the posterior overhang. *Schizaster dumblei* Israelsky (1924, p. 141), originally figured in Dickerson and Kew (1917, pl. 18, fig. 2; pl. 19, fig. 2; pl. 20, fig. 2) as *S. scherzeri* Gabb, has a more central apical system and shorter anterior paired petals. It was described from Dumble's San Rafael beds, now considered part of the Mesón formation (Muir, 1936, p. 133) of the Tampico region. Arnold and Clark (1927, p. 60, pl. 12, figs. 5,6) have recorded *S. dumblei* from the Spring Mount district of Jamaica.

Genus BRISSOPSIS L. Agassiz, 1840
Type species: BRISSOPSIS ELEGANS L. Agassiz

BRISSOPSIS n. sp.
Pl. 67, figs. 4,7; pl. 68, fig. 5; text-fig. 1,D; text-fig. 2,B.

Test missing anterior one-fourth, slightly crushed; moderately large, elongated; posterior truncated, periproct at top of truncation; apical system apparently slightly anterior; genital pores not apparent; posterior petals confluent for about half their length, deeply incised; anterior lateral petals not as deep; anterior petal deeply incised; position of peristome uncertain, but anterior; plastron with a moderate keel posteriorly.

Dimensions of hypotype: length (incomplete) 68 mm.; width (crushed) 54 mm.; height (crushed laterally) 35 mm.

Hypotype, U. S. Nat. Mus. no. 563462.

The specimen is not complete enough to furnish the basis for an adequate description. There does not seem to be any closely comparable New World fossil species, but it is probably referrable to the group of *Brissopsis lyrifera* (Forbes), the type of *Kleinia* Gray, 1851. Mortensen (1951, p. 371–375) says that there are all intermediates between typical *Brissopsis* and typical *Kleinia*. *Brissopsis blanpiedi* Grant and Hertlein (see Cooke, 1942, p. 49, pl. 5, figs. 23–28) is a somewhat similar type from the middle Oligocene of Mississippi.

Genus SCHIZOBRISSUS Pomel, 1869
Type species BRISSUS CRUCIATUS L. Agassiz

SCHIZOBRISSUS KEWI n. sp.
Pl. 67, figs. 2,6,9; text-fig. 1,B.E; text-fig. 2,C.

Test moderately large, surface largely abraded; outline elongate cordate, anterior depression shallow; apical system about three-eights distance from anterior end, elevated; paired petals elongate, moderately depressed; anterior petal broader but about equally depressed; peripetalous fasciole not well preserved but indented between anterior and posterior petals; genital pores four; median depression in apical system extending into posterior interambu-

EXPLANATION OF PLATE 67

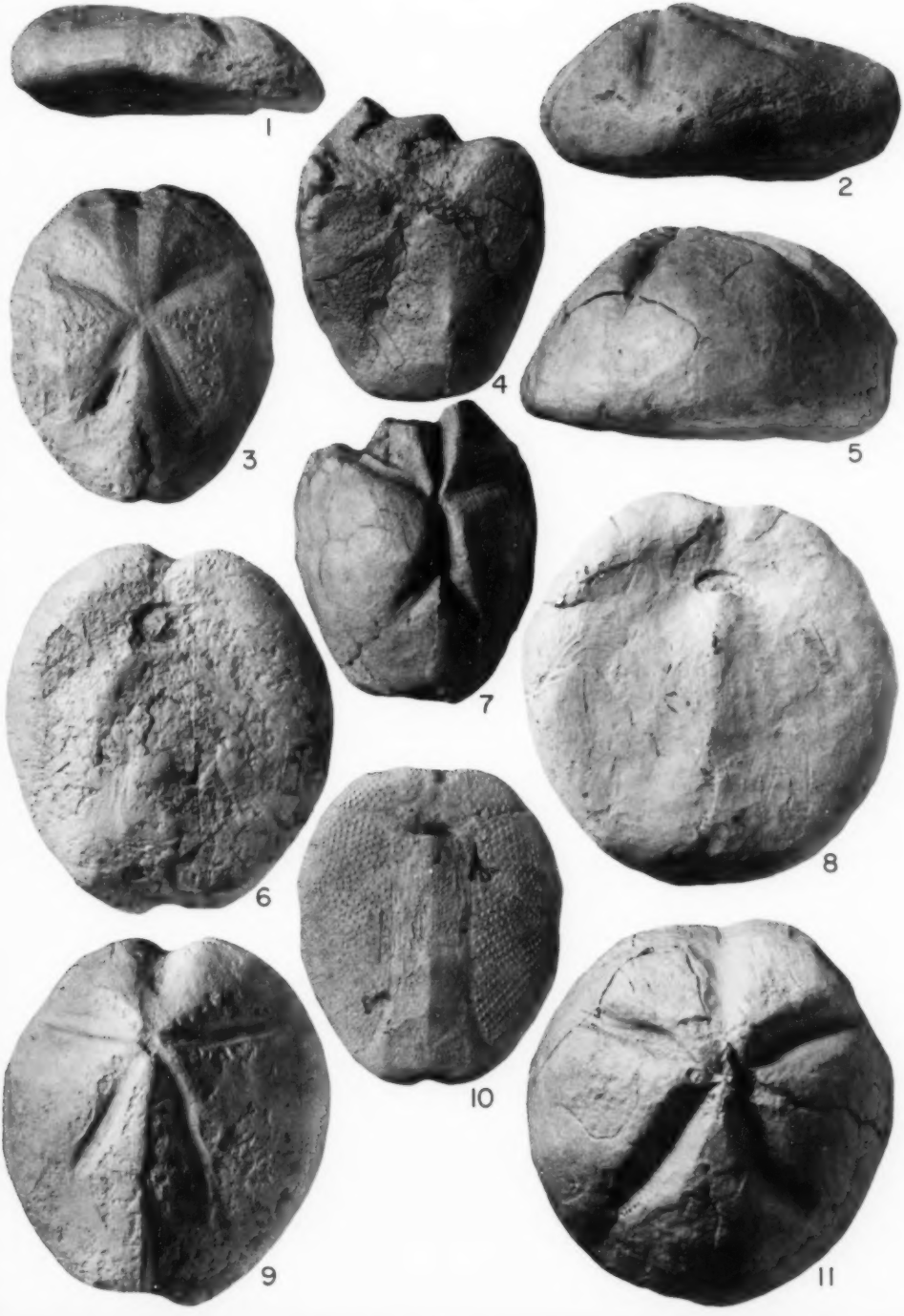
All magnifications ×0.75 approximately

FIGS. *1,3,10*—*Plagiobrissus malavassii* n. sp. Holotype, U. S. Nat. Mus. no. 563465. *1*, right lateral view. *3*, apical view. *10*, oral view.

2,6,9—*Schizobrissus kewi* n. sp. Holotype, U. S. Nat. Mus. no. 563463. *2*, left lateral view. *6*, oral view. *9*, apical view.

4,7—*Brissopsis* n. sp. Hypotype, U. S. Nat. Mus. no. 563462. *4*, oral view. *7*, apical view.

5,8,11—*Pericosmus israelskyi* n. sp. Holotype, U. S. Nat. Mus. no. 563458. *5*, left lateral view. *8*, oral view. *11*, apical view.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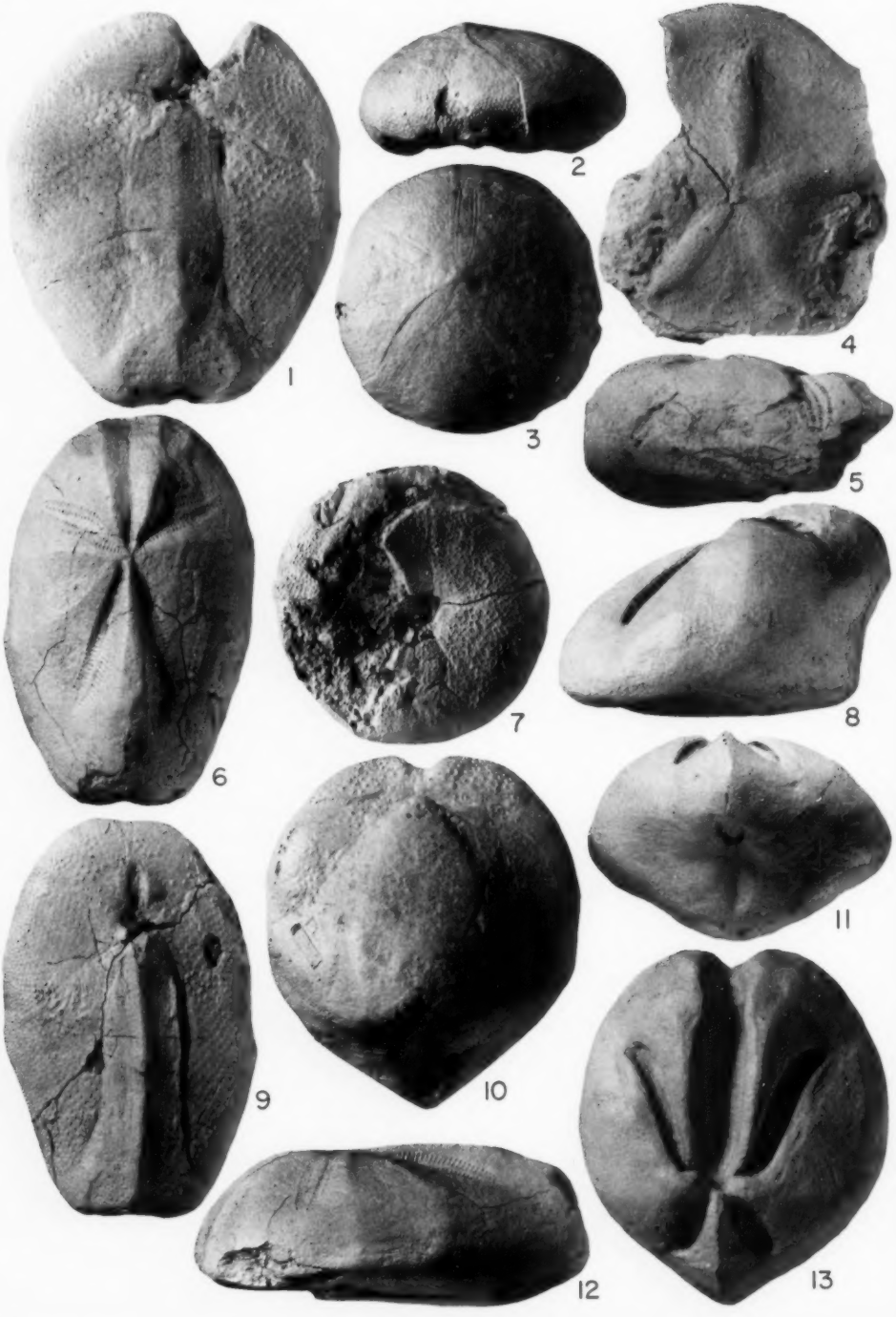
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lacrum; posterior interambulacrum fractured, but with moderately developed aboral keel; posterior end truncated, slightly overhanging; periproct moderately large, at top of truncation; peristome well anterior, margin incomplete; plastron poorly preserved.

Dimensions of holotype: length 82 mm., width 72.2 mm., height 39.5 mm.

Holotype, U. S. Nat. Mus. no. 563463.

This species resembles *Macropneustes dubius* Israelsky (1924, p. 143–144, pl. 3, fig. 1), a new name for *M. antillarum* Cotteau of Dickerson and Kew (1917, pl. 24, fig. 1, pl. 26, figs. 1a–1b) *non* Cotteau, from the Tuxpan formation of the Tampico region but differs from it by its less inflated test, shorter posterior petals, and more nearly straight anterior paired petals. The peripetalous fasciole is only preserved in a few places on the single specimen but it clearly had a trace similar to that of Israelsky's type and to that shown by Cotteau (1875, p. 39, pl. 7, figs. 1–3) for his original *Peripneustes antillarum*.

Israelsky (1924, p. 144) noted that his species and Cotteau's did not seem to be typical *Macropneustes* and suggested that they should be removed from the genus. Cotteau's *antillarum* was the type of his *Peripneustes* which has been placed in the synonomy of the earlier *Schizobrissus* Pomel. The embayment of the peripetalous fasciole between the petals seems to form a sound basis for separation of *Schizobrissus* from *Macropneustes*.

Genus PLAGIOBRISSUS Pomel, 1883

Type species: ECHINUS GRANDIS Gmelin

PLAGIOBRISSUS COSTARICENSIS n. sp.

Pl. 68, figs. 6,9,12; text-fig. 1,G,J; text-fig. 2,F.

Test large, elongate ovoid, slightly crushed laterally; apical surface inflated, posterior interambulacrum raised to a rounded keel; apical system slightly over one-third distance from anterior end; paired petals only slightly depressed except where distorted by crushing; anterior petal slightly depressed, with minor keel-like ridges adjacent to it; posterior end truncated, eroded, apparently not overhanging; plastron long and narrow, with well developed median keel; peristome small, slightly over one-fourth distance from anterior end; peripetalous fasciole approximately parallel to ambitus; apical system confused by crushing; large aboral primary tubercles worn, confined inside peripetalous fasciole, and continuous between paired petals; pores in outer row in paired petals slightly more elongate than in inner row.

Dimensions of holotype (crushed laterally) length 96.6 mm., width 55.5 mm., height 37.2 mm.

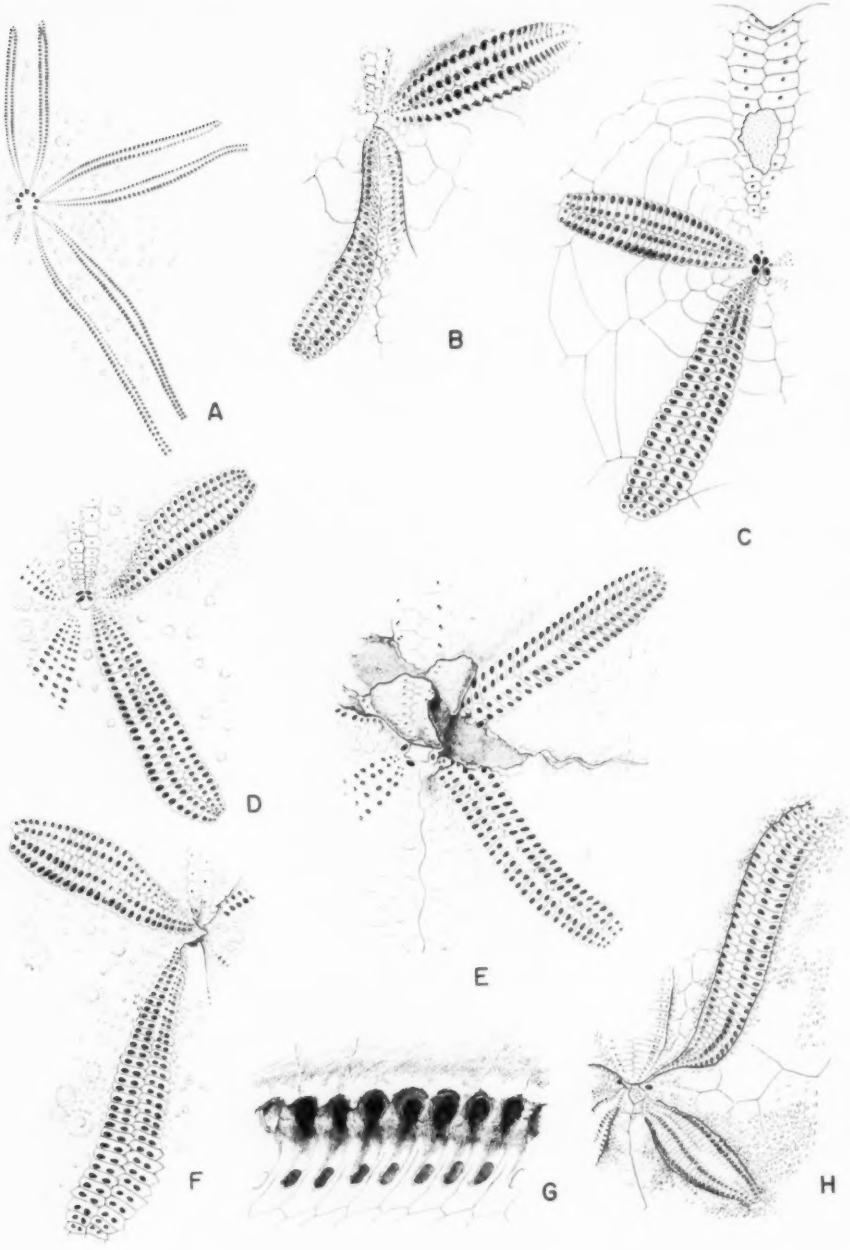
Holotype, U. S. Nat. Mus. no. 563464.

The single available specimen is obviously slightly compressed laterally but the less eccentric apical system and peristome clearly separate it from the associated *Plagiobrissus malavassii* n. sp. No described

EXPLANATION OF PLATE 68

All magnifications ×0.75 approximately

FIG. *1*—*Plagiobrissus malvaassii* n. sp. Paratype, U. S. Nat. Mus. no. 563466. Oral view.
2,3,7—*Echinolampus woodringi* n. sp. Holotype, U. S. Nat. Mus. no. 563454. *2*, left lateral view. *3*, apical view. *7*, oral view.
4—*Clypeaster* sp. indet. Hypotype, U. S. Nat. Mus. no. 563456. Apical view.
5—*Brissopsis* n. sp. Hypotype, U. S. Nat. Mus. no. 563462. Right lateral view.
6,9,12—*Plagiobrissus costaricensis* n. sp. Holotype, U. S. Nat. Mus. no. 563464. *6*, apical view. *9*, oral view. *12*, right lateral view.
8,10,11,13—*Schizaster costaricensis* n. sp. Holotype, U. S. Nat. Mus. no. 563459. *8*, left lateral view. *10*, oral view. *11*, posterior view. *13*, apical view.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species of the genus approaches it in the degree of elongation and the inflated apical surface.

PLAGIOBRISSUS MALAVASSII n. sp.
Pl. 67, figs. 1,3,10; Pl. 68; fig. 1;
text-fig. 1,H,K; text-fig. 2,D.

Test large, outline ovoid, moderately flattened; posterior truncated, with slight overhang; paired petals moderatly depressed; anterior petal only slightly depressed; apical system nearly two-fifths distance from anterior end; posterior interambulacrum slightly raised on aboral surface; peripetalous fasciole not well preserved but approximately parallel to margin of test; peristome about one-fifth distance from anterior end; plastron long, moderately narrow, ridged; subanal fasciole enclosing a cordate area with a typical radiate arrangement of pore pairs; periproct pyriform, on posterior truncation, not visible from above; large adapical tubercles all within peripetalous fasciole, continuous across area between paired petals; outer row of pores in petals more elongate than pores in inner row.

Dimensions: Holotype, length 69.8 mm., width 58.4 mm., height 25.1 mm.; paratype, length (estimated) 88 mm., width 73.3 mm., height 28.5 mm.

Types: Holotype, U. S. Nat. Mus. no. 563465; paratype, U. S. Nat. Mus. no. 563466.

This species may be related to *P. lamberti* Jeannet (1928, p. 38–41, pl. 5, figs. 1,2; text-fig. 12), which was founded on a very incomplete specimen, but seemingly is more elongate. *Plagiobrissus loveni* (Cotteau) (1875, p. 41–42, pl. 8, figs. 7,8) has a more central apical system. The various Eocene species (*dixie, gardnerae, carolinensis, curvus,* and *ocalanus*) referred to *Eupatagus* (*Plagiobrissus*) by Cooke (1942) all have a less eccentric peristome. *Metalia cumminsi* Kew (in Dickerson and Kew, 1917, p. 133–134, pl. 22, fig. 1, pl. 23, fig. 1) which was referred to *Plagiobrissus* by Israelsky (1924, p. 144) is referrable to the genus *Lajanaster* Lambert and Sanchez Roig, characterized by a restriction of the large primary tubercles inside the peripetalous fasciole to the areas immediately adjacent to the petals. The living *Plagiobrissus grandis* (Gmelin) and *P. africanus* (Verrill) have a more central apical system.

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TEXT-FIG. 2-*A*.—*Echinolampas woodringi* n. sp. ×1.5. Holotype, U. S. Nat. Mus. no. 563454; *B*.—*Brissopsis* n. sp. ×1.5. Hypotype, U. S. Nat. Mus. no. 563462; *C*.—*Schizobrissus kewi* n. sp. ×1.5. Holotype, U. S. Nat. Mus no. 563463; *D*.—*Plagiobrissus malavassii* n. sp. ×1.5. Holotype, U. S. Nat. Mus. no. 563465; *E*.—*Pericosmus israelskyi* n. sp. ×1.5. Holotype, U. S. Nat. Mus. no. 563458; *F*.—*Plagiobrissus costaricensis* n. sp. ×1.5. Holotype, U. S. Nat. Mus. no. 563464; *G, H*.—*Schizaster costaricensis* n. sp. *G*, paratype, U. S. Nat. Mus. no. 563460, ×5, detail of part of left side of left posterior petal. *H*, Holotype, U. S. Nat. Mus. no. 563459, ×1.5.

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JOURNAL OF PALEONTOLOGY, V. 35, NO. 3, P. 489–497, PLS. 69–70, 1 TEXT-FIG., MAY, 1961

MIOCENE FORAMINIFERA, MOLLUSKS, AND A BARNACLE FROM THE VALLE CENTRAL, COSTA RICA*

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ABSTRACT—For many years middle Tertiary fossils have been known to occur in the Valle Central of Costa Rica. Siltstone at a locality near Turrúcares, 25 kilometers west of San José and at an altitude of 640 meters above sea level, recently yielded Foraminifera. Mollusks, a barnacle and echinoids were found in sandstone conformably overlying the siltstone. The Foraminifera are listed, and the mollusks and barnacle are briefly described. These fossils are of Miocene age. The Foraminifera suggest middle Miocene; the mollusks indicate early or middle Miocene.

INTRODUCTION

THE purpose of the present paper is to describe and list Miocene marine fossils collected at a locality near Turrúcares in the Valle Central of Costa Rica, formerly known as the Meseta Central. Middle Tertiary fossils have been found at scattered places in central Costa Rica, but the locality near Turrúcares, 25 kilometers west of San José, yielded the best material so far known.

The stratigraphy at the fossil locality is described by Malavassi, who also contributed the list of Foraminifera. Woodring prepared the review of fossil localities, the description of the mollusks and barnacle and the discussion of age. The echinoids associated with the molusks and barnacle are described by Durham (1961) in an accompanying paper.

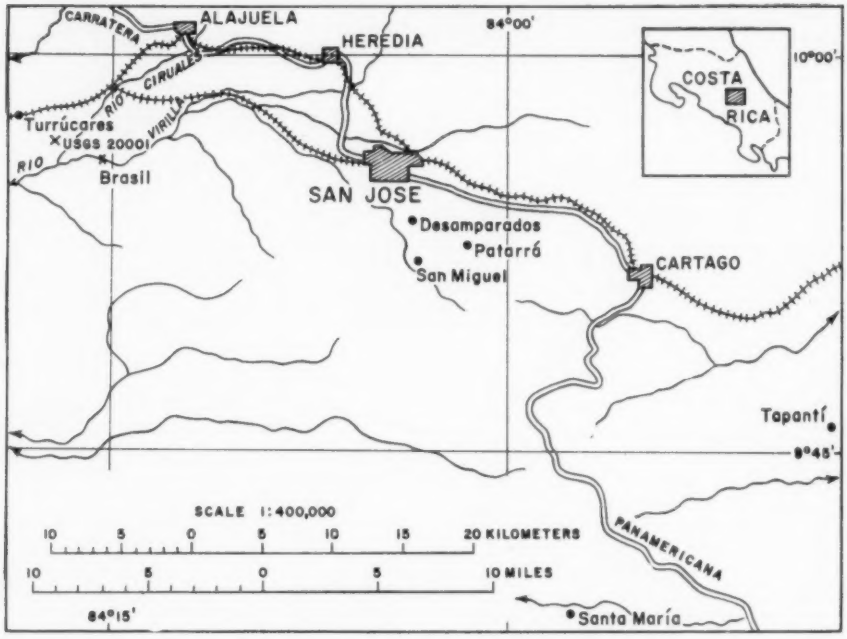
P. J. Bermúdez, of the Creole Petroleum Corporation, kindly reviewed the identification of the Foraminifera.

Fossil localities in Valle Central and nearby

The localities where middle Tertiary fossils have been found in the Valle Central and nearby are shown in Text-fig. 1. The earliest record was published by Hill (1898, p. 226–227). He found fossils at quarries in "massive blue-black Paleozoic-looking limestone" near the villages of San Miguel and Desamparados, in the western foothills of the Cerros de Candelaria, which form part of the boundary between the Valle Central Occidental and the Valle Central Oriental. Though Hill recognized a large pectinid of Tertiary aspect, he thought polished surfaces of the limestone showed fragments of rudists and *Inoceramus*, and therefore considered the limestone to be of Cretaceous age. Romanes (1912, p. 107–108) confirmed the occurrence of a large pectinid in the limestone and observed a small pectinid, a small oyster, and barnacles of the genus *Balanus*. He was unable to confirm Hill's identification of Cretaceous fossils and concluded that the limestone is Tertiary. Romanes' age determination is supported by collections in the U. S. National Museum. Romanes (1912, p. 118–119) also found fossils in conglomerate and tuff at Brasil, on Río Virilla: pectinids and poorly preserved gastropods.

Don Anastasio Alfaro (1911, p. 126–129), at that time Director of the Museo Nacional in San José, recorded the occurrence of marine mollusks at Patarrá, Desamparados, south of Turrúcares, and on the slope above Río Virilla at Brasil; and fresh-water gastropods in the tunnel for the hydroelectric project at Brasil. Later he again described the occurrence of fresh-water gastropods in the tunnel (Alfaro, 1913, p. 859). Lohmann (1934, p. 14) recorded pectinids and *Pyrula* [*Ficus*] between Turrúcares and Río Virilla —that is, probably near the locality that yielded the fossils described in the present paper—and Crosby (1942, p. 487) noted pectinids in tuff at Brasil. Without realizing

* Publication authorized by the Director, U. S. Geological Survey and the Jefe, Departamento de Geología, Minas y Petróleo.



TEXT-FIG. 1—Map showing middle Tertiary fossil localities in Valle Central and adjoining parts of Costa Rica. Base from 1:400,000 map of Costa Rica issued by Instituto Geográfico de Costa Rica, 1949.

it, Haas (1942, p. 310 [nos. 30–33], 315–316) contributed to what is known about Alfaro's fresh-water gastropods from the tunnel at Brasil. Haas, however, ascribed them to marine genera (Woodring, 1957–59, p. 110, 1957). A small form of *Clementia dariena*, collected by J. F. Tristan at Santa María, south of the Valle Central, was forwarded to the U. S. National Museum by Alfaro (Woodring, 1926, p. 36).

Early collections deposited in the U. S. National Museum are summarized in the following table. Most of the undetermined species in these collections are, in fact, indeterminable.

LOCALITY NEAR TURRÚCARES (USGS 20001)

The locality, where the fossils described in the present paper were collected by Malavassi in 1957, is 2.9 kilometers south-southeast of the railroad crossing at Turrúcares, at an altitude of 640 meters above sea level on the east slope of a ridge trending northeastward parallel to Río Ciruelas, a tributary of Río Virilla (Text-fig. 1). It also is 250 meters southeast of Candelaria triangulation station shown on the 1:25,000 Turrúcares topographic map of the Instituto Geográfico de Costa Rica. Malavassi's collection is entered as USGS 20001. Additional specimens, collected by Malavassi, A. A. Olsson, Rodrigo Sáenz, and Woodring in 1958, are entered as USGS 21235.

The stratigraphic succession at locality 20001 is as follows:

STRATIGRAPHIC SECTION AT USGS LOCALITY 20001 NEAR TURRÚCARES

	meters
Andesitic intrusive rock	
Miocene(?)	
4. Tuffaceous siltstone and sandstone, altered by intrusive rock	7

U. S. NATIONAL MUSEUM COLLECTIONS OF FOSSILS FROM VALLE CENTRAL AND ADJOINING PARTS OF COSTA RICA

Locality	Species
USGS 5466, 7292b, Cerro de los Turrúcares. Anastasio Alfaro, 1910.	*Pecten* (*Flabellipecten?*) sp., *Aequipecten* sp.
USGS 5506, 7292a, Turrúcares. Anastasio Alfaro, 1910.	*Aequipecten* sp., *Crassatella* cf. *C. deformis* Heilprin.
USGS 5509, Narajo, 5 km south of Turrúcares. Anastasio Alfaro, 1909.	*Turritella* (*Torcula*) *altilira* Conrad, subsp.
USGS 5505, Brasil. Anastasio Alfaro, 1910.	*Semicassis?* sp., *Gemmula?* sp., *Pecten* (*Pecten*) sp., *Aequipecten* sp., *Trachycardium* sp., *Chione?* sp.
USGS 5467, Tunnel at Brasil. Anastasio Alfaro, 1910.	*Pachychilus* aff. *P. atratus* Pilsbry and Hinkley, *Hemisinus altispirus* (Haas).
USGS 5502, Tunnel at Brasil, 900 feet from entrance. Anastasio Alfaro, 1910.	*Pachychilus? tarataranoides* (Haas), *Hemisinus altispirus* (Haas), *Trachycardium* aff. *T. dominicense* (Gabb).
USGS 7282, Brasil. J. F. Tristan, 1910.	*Pachychilus? tarataranoides* (Haas).
USNM cat. no. 6465, 6469, San Antonio. J. H. Lohman, 1867.	*Lyropecten?* (*Nodipecten?*) sp., *Aequipecten* sp., *Balanus?* sp.
USGS 7291. San Antonio de Desamparados. Anastasio Alfaro, 1910.	*Lyropecten* (*Nodipecten*) cf. *L. nodosus* (Linné), *Balanus?* sp.
USGS 5504, Patarrá. Anastasio Alfaro, 1910.	*Lyropecten* (*Nodipecten*) cf. *L. nodosus* (Linné), *Balanus?* sp.
USGS 18691, Chucheca, Patarrá. Anastasio Alfaro, 1910.	*Crassostrea?* sp.
USGS 18697. Tapantí. Received from Museo Nacional, 1910?	*Aequipecten* sp.
USGS 7274–7279, Santa María de Dota. J. F. Tristan, 1909.	*Turritella* sp., *Natica?* sp., *Pecten* (*Flabellipecten?*) sp., *Aequipecten* sp., *Miltha* sp., *Clementia dariena* (Conrad), small form.

Miocene
3. Fossiliferous, somewhat calcareous, medium-grained sandstone and coarse grained sandstone, including conglomeratic layers. Contains mollusks, barnacle and echinoids 25
2. Fine-grained sandstone and foraminiferal sandy siltstone 110

Unconformity

Upper Oligocene(?)
1. Black, calcareous siltstone and silty mudstone containing a few Foraminifera 38

On the west slope of the ridge the andesitic intrusive rock is overlain by diatomite, tuff, and volcanic ash. According to a communication from K. E. Lohman, of the U. S. Geological Survey, who identified 25 species of diatoms in two samples, these strata are of Pleistocene age.

FORAMINIFERA FROM UNIT 2 AT USGS LOCALITY 20001

[Identifications by Enrique Malavassi V.; A, abundant; C, common; F, few; R, rare]

Biorbulina bilobata (d'Orbigny)	A
Bolivina marginata var. *multicostata* Cushman	A
Bolivina imporcata Cushman and Renz	A
Bulimina cf. *B. tessellata* Cushman and Todd	R
Bulimina cf. *B. uvigerinaformis* Cushman and Kleinpell	F
Frondicularia sp. (fragments)	R
Globigerina bulloides d'Orbigny	A
Globigerinoides cf. *G. ruber* (d'Orbigny)	A
Globigerinoides transitorius Blow	A
Globigerinoides trilobus (Reuss)	A
Globobulimina pacifica Cushman	A

Globoquadrina altispira (Cushman and Jarvis)	A
Orbulina suturalis Bronnimann	A
Nonion costiferum (Cushman)	R
Plectofrondicularia sp. (fragments)	R
Rectoglandulina sp.	R
Robulus sp.	C
Saracenaria sp.	R
Siphogenerina lamellata Cushman	R
Turborotalia mayeri (Cushman and Ellisor)	C
Uvigerina peregrina Cushman	F

MOLLUSKS AND BARNACLE

Unit 3 yielded the mollusks and barnacle, as well as the echinoids described by Durham in an accompanying paper.

The original shell material is preserved only on the calcite-shelled mollusks (pectinids and ostreid). On some of the aragonite-shelled forms, however, the aragonite is recrystallized to calcite.

TURRITELLA (TORCULA) ALTILIRA Conrad, subspecies

Pl. 69, fig. 3

?*Turritella altilirata* [error for *altilira*] Conrad, Gabb, 1881, p. 341, pl. 44, fig. 9; not fig. 9a (= *T. sapotensis* Brown and Pilsbry); Miocene, Costa Rica.

Ten specimens, each consisting of a few whorls, represent a subspecies of *Turritella altilira* characterized by heavy, strongly noded anterior and posterior primary spirals of practically equal width. A weakly noded minor spiral lies in front of the anterior primary spiral, but other minor spirals are obscure. The figured specimen of five whorls (height 38.7 mm., diameter 13 mm.) is in the best condition. It is, however, somewhat crushed, and in the view shown on plate 69, figure 3, the diameter is slightly reduced by crushing.

Gabb found his *T. "altilirata"* at Sapote on Río Reventazón, in deposits that are considered of early Miocene age. Though the locality he designated Sapote can no longer be identified, it evidently was near Las Lomas, about 80 kilometers east-northeast of Turrúcares. Both of his illustrations suggest a subspecies of *T. altilira* like that at locality 20001; indeed, the specimen represented by his figure 9 may be that form. The primary spirals of that specimen are of practically equal width. Though they are lower—especially the anterior one—than those of the specimen illustrated in the present paper, they are hardly lower than those of several others collected at locality 20001. Gabb's other specimen, incorrectly shown in his figure 9a, is a different species which has been named *T. sapotensis* (Brown and Pilsbry, 1911, p. 359, pl. 27, fig. 10). The sculptural plan, growth-line sinus and growth-line angle indicate that *T. sapotensis* is an exceptional species of the group of *T. altilira* that lacks a posterior primary spiral.

Subspecies of *T. altilira* are found throughout the Caribbean region in deposits ranging in age from late Oligocene to early Pliocene. Though many names have been proposed for different forms, their geographic and age relations have not been worked out. On the adequately described early forms—such as an unnamed late Oligocene subspecies from the Caimito formation of the Canal Zone (Woodring, 1957–59, p. 104, pl. 15, fig. 10, 1957) and *T. altilira praecellens* (Pilsbry and Brown, 1917, p. 36, footnote, pl. 5, fig. 12), which occurs in the late early Miocene Baitoa formation of the Dominican Republic and also in the early middle Miocene part of the Gatun formation of Panamá (Woodring, 1957–59, p. 105, pl. 23, figs. 2,8, 1957)—the posterior primary spiral is wider than

EXPLANATION OF PLATE 69

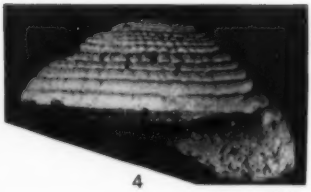
Specimens from USGS locality 12001 near Turrúcares, Costa Rica. Photographs natural size unless otherwise specified.

FIGS. *1,2*—*Cypraecassis* cf. *C. tenuis* (Wood), USNM 563648.
3—*Turritella* (*Torcula*) *altilira* Conrad, subsp., ×1½, USNM 563647.
4–6—*Architectonica* (*Architectonica*) *nobilis nobilis* Röding, ×1½, USNM 563650.
7,8—*Malea* aff. *M. elliptica* Pilsbry and Johnson, USNM 563649.

1

2

3 X1½

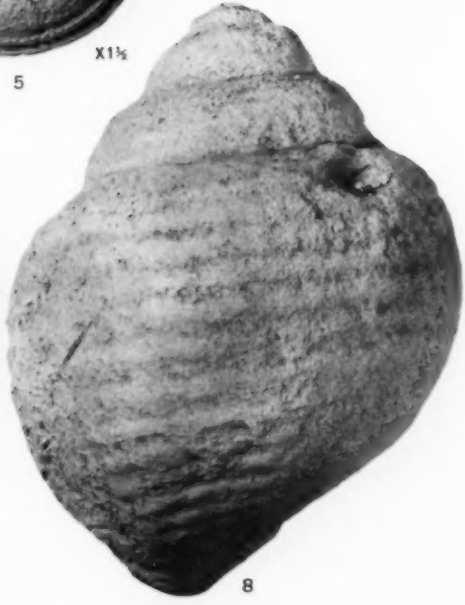


4 X1½

5 X1½

6 X1½

7



8

X1½
1
X1½
3
2
5
4

the anterior and generally is doubled. Such forms evidently lead to the nominate subspecies, which first appeared in late early Miocene deposits in Panamá and is abundant in the late middle Miocene part of the Gatun formation. The typical form has flange-like primary spirals. The posterior one is almost invariably wider than the anterior and, with few exceptions, is unequally doubled (Woodring, 1957–59, p. 102, pl. 23, figs. 1,7,12,13, 1957).

T. crocus (Cooke, 1919, p. 121, pl. 4, fig. 8) doubtless is a form of *T. altilira* and may have practically equal primary spirals. It occurs in the Anguilla formation of the island of Anguilla, assigned to the early part of the early Miocene, and possibly also in the late Oligocene Antigua formation of the island of Antigua. The type—the only available specimen from the Anguilla formation—is an internal mold of four whorls. Until adequate topotype material is available, *T. crocus* may be treated as a *nomen dubium*. A three-whorled fragment from Antigua, labelled *Turritella* cf. *T. crocus*, has some recrystallized shell material. The primary spirals are subequal, but are narrower than those of the specimens from locality 20001.

Late forms of *T. altilira* also have subequal primary spirals: *T. altilira guppyi* Cossmann (Woodring, 1928, p. 349, pl. 26, figs. 7,8, not fig. 9; late middle Miocene, Bowden formation, Jamaica) and *T. altilira chiriquiensis* (Olsson, 1922, p. 150, pl. 14, figs. 4,8,9,14; late middle and late Miocene, southeastern Costa Rica and northwestern Panamá). These forms, however, have subdued primary spirals. The late Miocene specimen from Water Cay [Cayo de Agua, Archipiélago de Bocas del Toro, northwestern Panamá], illustrated by Olsson as figure 8 is herewith designated the lectotype of *T. altilira chiriquiensis*. That form is so similar to *T. altilira guppyi* that perhaps the name is to be suppressed.

ARCHITECTONICA (ARCHITECTONICA) NOBILIS NOBILIS Röding
Pl. 69, fig. 4–6

Architectonica nobilis Röding, 1798, p. 78; Recent, locality unknown.

Solarium granulatum Lamarck, 1822 p. 3; Recent, locality unknown.

Architectonica (*Architectonica*) *nobilis nobilis* Röding, Woodring, 1957–59, p. 165, pl. 29, figs. 1–6,10–12,14–16, 1959; Miocene, Panamá; additional citations.

Two specimens are referred to the nominate subspecies of *Architectonica nobilis*. The larger has a height of about 14.5 mm. and a diameter of 35 mm.; the same dimensions of the smaller, which is illustrated, are 15.5 mm. and 29.2 mm., respectively. Though these fossils are not well preserved, the smaller shows the sculptural pattern of *A. nobilis nobilis:* a peripheral cord, four closely spaced dorsal cords and six closely spaced ventral cords, all cut into flat, closely spaced nodes by narrow axial grooves, except the relatively wide umbilical cord which is coarsely corrugated. On the later part of the body whorl the nodes are suppressed on the peripheral and dorsal cords, and also on the fourth and fifth ventral cords beyond the umbilical cord. On the body whorl a secondary thread lies between the peripheral cord and the first dorsal cord, as on some other fossil specimens and many Recent specimens (Woodring, 1957–59, p. 166, 1959).

A. nobilis nobilis is one of the relatively few forms widely recognized as surviving in both western Atlantic and eastern Pacific waters. *Murex recurvirostris recurvirostris* is

EXPLANATION OF PLATE 70

Specimens from USGS locality 12001 near Turrúcares, Costa Rica. Photographs natural size unless otherwise specified.

FIGS. *1,3—Aequipecten* aff. *A. plurinominis* (Pilsbry and Johnson), ×1½, USNM 563652.
2–5—Pecten (*Flabellipecten*) *gatunensis gatunensis* Toula, large form, USNM 563651.

another example (Woodring, 1957–59, p. 214, 1959). Both forms appeared in early Miocene time, when the Tertiary Caribbean Province embraced both western Atlantic and eastern Pacific waters. The early Miocene specimens of *A. nobilis nobilis* generally are smaller than those of middle Miocene and later age.

Cypraecassis cf. C. tenuis (Wood)
Pl. 69, figs. 1,2

A mold of a moderately large cassid (almost complete height 74.7 mm., diameter 46 mm.) is assigned to the genus *Cypraecassis*, though the apertural features are missing. A little recrystallized shell material attached to the mold shows that the sculpture consists of relatively widely spaced and relatively narrow spiral bands. Remnants of low tubercles are visible on part of the shoulder, but not elsewhere. The sculpture, though meagerly preserved, indicates that this species, probably a new species, is more closely related to the Recent Panamic *C. tenuis* (Wood) than to the Recent Caribbean *C. testiculus* (Linné), which has closely spaced axial threads and weak spiral sculpture. *C. tenuis*, however, is sculptured with closely spaced spiral bands of varying width. Three wide bands below the shoulder, as well as the shoulder band, bear tubercles or swellings.

The genus *Cypraecassis* is very rare in the Tertiary deposits of the Caribbean region. In fact, the small Miocene specimens of *C. testiculus* collected by Gabb 90 years ago in the Dominican Republic (Pilsbry, 1922, p. 361), are the only other representatives so far found.

Malea sp. aff. M. elliptica Pilsbry and Johnson
Pl. 69, figs. 7,8

A mold of a moderately large (almost complete height 93.5 mm., diameter 70 mm.), inflated, high-spired *Malea* and a less complete mold of comparable size are identified as *Malea* aff. *M. elliptica*. The constriction of the body whorl as the missing outer lip is approached shows that this tonnid is to be referred to *Malea*, not *Tonna*. Wide spiral bands, separated by grooves about half as wide, are impressed on part of the body whorl of the more complete mold. *M. elliptica* (Pilsbry, 1922, p. 363, pl. 29, fig. 3), found by Gabb at an unrecorded Miocene locality in the Dominican Republic is high-spired, unlike the other species of the Tertiary Caribbean province. It is more slender than the Costa Rican form.

An immature unarmed tonnid, from the middle Miocene part of the Gatun formation of the Canal Zone, probably is allied to *M. elliptica* (Woodring, 1957–59, p. 209, 1959).

Malea is one of the numerous genera that formerly lived in the ancestral Caribbean Sea and the ancestral eastern Pacific Ocean, but now survives in the eastern Pacific Panamic province.

Pecten (Flabellipecten) gatunensis gatunensis Toula, large form
Pl. 70, figs. 2,4,5

Pecten (Flabellipecten) gatunensis Toula, 1909, p. 711, pl. 26, fig. 2; Miocene, Canal Zone.
Pecten sp., Toula, 1909, p. 755, text-figs., 12,13; Miocene, Canal Zone.
Pecten flabelliformis Defrance, Toula, 1909, p. 756, text fig. 14; Miocene, Canal Zone.
Pecten gatunensis Toula, Brown and Pilsbry, 1911, p. 365; Miocene, Canal Zone; Hodson, Hodson, and Harris, 1927, p. 24; Miocene, Falcón, Venezuela.
Pecten (Pecten) gatunensis Toula, Olsson, 1922, p. 197, pl. 16, figs. 3,4; Miocene, Canal Zone, northwestern Panamá.

Seven specimens, all incomplete, are referred to the large form of *Pecten gatunensis gatunensis* found in the late early Miocene Alhajuela sandstone member of the Caimito formation of Madden basin, Panamá. The two largest specimens, which also are in the best state of preservation, are illustrated. Their dimensions are as follows: incomplete length 79 mm., incomplete height 77 mm., diameter (both valves) 14 mm. pl. 70, figs. 2,4); incomplete length 99 mm., incomplete height 88 mm., diameter (both valves) 15.5 mm. (pl. 70, fig. 5). The approximate restored dimensions are 95 mm. by 90 mm. and 110 mm. by 105 mm., respectively. The right valve is moderately inflated and sculptured with 20 to 22 strong, relatively closely spaced, wide, flat ribs; the left valve is almost flat and sculptured with 18 or 19 widely spaced, narrow, somewhat rounded ribs. The auricles are missing or imperfectly preserved and the interior is inaccessible.

All the specimens are somewhat worn and the delicate, closely spaced concentric lamellae of perfectly preserved specimens, represented on these fossils by faint remnants on parts of the shell, are almost indiscernible on the photographs.

Toula's fossils were found in the late middle Miocene part of the Gatun formation of the Canal Zone. In the Canal Zone and adjoining parts of Panamá, however, the lineage of *P. gatunensis* occurs in deposits of late Oligocene to early Pliocene age. The nominate subspecies and the form in the early Pliocene Toro limestone member of the Chagres sandstone—*P. macdonaldi* (Olsson, 1922, p. 198, pl. 16, figs. 1,2), which is to be treated as a subspecies of *P. gatunensis*—have been named and described. The nominate subspecies has ribs on the right valve that continue to the margin with undiminished strength. It is widespread in the middle part of the Gatun formation and also occurs in the early middle Miocene lower part of the formation. The largest specimens from the Gatun have a length of 75 to almost 80 mm. The fossils from the locality near Turrúcares closely resemble the large form of *P. gatunensis gatunensis* (maximum length 115 mm.) that is found in the Alhajuela sandstone member of the Caimito formation.

Though it has recently been denied that *Flabellipecten* reached American waters (Mongin, 1959, p. 303–304), *P. gatunensis* seems to be properly referred to *Flabellipecten* (Sacco, 1897, p. 55; originally designated type, *Ostrea flabelliformis* Brocchi, Miocene and Pliocene, Italy), where it was placed 50 years ago by Toula. The right valve of *P. gatunensis* is not as inflated as that of the type species and the left valve has more rounded ribs and no midrib in the interrib spaces. Moreover, the middle pair of the three pairs of cardinal crura of *P. flabelliformis* is represented only by a swelling or is absent, at least on the typical small form of *P. gatunensis gatunensis*. The crura of both species bear microscopic somewhat vermicular sculpture found in *Pecten* s.s. and other groups of pectinids. The inflation of the right valve of the European species of *Flabellipecten*, of Miocene and Pliocene age, is variable; a midrib is present or absent in the interrib spaces on the right valve; and the midrib of the left valve is of varying strength (Roger, 1943, p. 185–187).

A middle Miocene pectinid of medium size from western Florida has been identified as *P. macdonaldi* (Mansfield, 1932, p. 57, pl. 14, figs. 5,6). The identification is doubtful on the basis of the inadequate material now available. The ribs on the left valve of the Florida pectinid are wider than those of the much larger *P. gatunensis macdonaldi*.

LYROPECTEN? (NODIPECTEN?)
sp. cf. L. NODOSUS (Linné)

An incomplete mold of paired valves (incomplete length 78 mm., incomplete height 81 mm.) suggests a species of *Nodipecten* of moderately large size. The narrow ribs (9 visible on one valve and 11 on the other)—replicas of what is seen on the interior of shells—are irregularly undulated in a vertical plane. The undulations presumably were formed by exterior swellings and constrictions, like those of *Nodipecten*.

This pectinid is without much doubt the same as that, represented by more convincing molds, found in limestone at Desamparados and Patarrá (table on p. 491).

AEQUIPECTEN sp. aff. A. PLURINOMINIS
(Pilsbry and Johnson)
Pl. 70, figs. 1,3

Fourteen specimens, all more or less incomplete, are identified as *Aequipecten* aff. *A. plurinominis*. Those on which the total number of ribs is determinable have 18 to 20 ribs. In the umbonal region secondary sculpture is lost through wear. Farther from the umbo the ribs bear scabrous concentric lamellae. Still farther, in the ventral part of mature shells, the lamellae break up into minute scales arranged along very narrow radial threads on the ribs and in the spaces between them. Both valves illustrated are right valves (larger: incomplete length 36 mm., incomplete height 40.5 mm., diameter about 10 mm.; smaller: practically complete length and height 30.5 mm., diameter about 9 mm.).

The strongly inflated valves of this pectinid indicate that it is more closely related to a form of *A. plurinominis* (Pilsbry and Johnson) (Pilsbry, 1922, p. 411, pl. 45, figs. 1,2) found in the middle Miocene Gatun formation of the Canal Zone than to *A.*

canalis (Brown and Pilsbry) (1913, p. 511, pl. 24, fig. 3), which occurs in the lower Miocene Emperador limestone member of the Culebra formation in the Canal Zone.

INDETERMINABLE MOLLUSKS

Indeterminable species of *Crassostrea?*, *Trachycardium*, *Trigonocardia?*, *Cyclinella?*, and *Ventricolaria?* are represented by fragments, molds, or coarsely recrystallized shell material.

BALANUS sp.

Some fifty worn specimens of a moderately large species of *Balanus* (height of largest specimen 47 mm., diameter 20 mm.) were collected at locality 20001. The opercular valves of this barnacle are unknown.

AGE OF FOSSILIFEROUS STRATA

The Foraminifera recovered at locality 20001 are of Miocene age and suggest middle Miocene. Most of the mollusks in the overlying sandstone are undiagnostic for an age other than Miocene. The large form of *Pecten gatunensis gatunensis* suggests early Miocene, whereas *Aequipecten* aff. *A. plurinominis* suggests middle Miocene. If the pectinid identified as *Lyropecten?* (*Nodipecten?*) cf. *L. nodosus* is indeed closely allied to the Recent *L. nodosus*, it also suggests middle Miocene, as it is larger than the known early Miocene species of *Nodipecten*. *Crassatella* cf. *C. deformis*, found by Alfaro near Turrúcares, on the contrary, has early Miocene affinities. There is little basis for comparison with coastal southeastern Costa Rica, where deposits of both early and middle Miocene age crop out (Olsson, 1922), or with Gabb's (1881) early Miocene Sapote fossils. Though the early collections from the Valle Central and nearby were formerly thought to be of early Miocene age (Woodring, 1928, p. 88), early or middle Miocene is the best that can be done with the mollusks from the locality near Turrúcares.

The localities in the Valle Central that have yielded marine fossils are paleogeographically important. They show that during at least part of Miocene time this segment of the Panamá land bridge was covered by the open sea. How far north and how far south the sea extended is not known at present. It may have extended uninterruptedly from southern Nicaragua to northwestern Colombia, or within that span it may have been broken into several parts by islands.

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SOME COSTA RICAN LARGER FORAMINIFERAL LOCALITIES

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ABSTRACT—Nineteen species of larger Foraminifera, of which two species are from the Upper Cretaceous, one from the middle Eocene, 11 from the upper Eocene and 4 from the upper Oligocene, are recorded from 10 Costa Rican localities. These faunas are correlated with other well known Caribbean localities.

INTRODUCTION

ALTHOUGH larger Foraminifera occur abundantly at various Upper Cretaceous, Eocene and Oligocene localities in Costa Rica, the faunas of only a few localities have been recorded in various publications. This note summarizes this information and records the faunas from several other localities (text-fig. 1).

The first species of *Lepidocyclina* described from Costa Rica was named *L. hilli* by Cushman (1920, p. 60). This specimen was collected by R. T. Hill from the Guallava limestone. Vaughan (1931, p. 41) subsequently ground one side of this specimen to the equatorial plane, thereby discovering it was a microspheric individual. It is impossible with the information known to classify this specimen.

Lohman and Brinckman (1931, p. 554) reported 8 species from the upper Eocene Las Animas limestone in the vicinity of Turrialba (loc. 7). Later, Cole (1953*b*, p. 749) recorded 9 species and one variety from 3 upper Eocene localities in this same area.

Drooger (1952, p. 26) described *Miogypsina tani* as a new species from material collected by Pedro J. Bermudez from an Oligocene outcrop below the bridge on the Reventazon river on the road between the villages of Chitaria and Peralta (loc. 8). Cole (1957, p. 320) proved that this species is a synonym of *Miogypsina* (*Miogypsina*) *antillea* (Cushman).

Specimens identified by Davis (in Harrison, 1953, p. 107) as *Pseudorbitoides* cf. *P. israelskyi* Vaughan and Cole occur in samples from Santa Elena Bay and Murcielago (loc. 1) in rocks of Upper Cretaceous age. In addition he reported the presence of upper Eocene larger Foraminifera from Las Ruedas, but gave only generic determinations. However, at another locality near Pozo de Los Patos he referred specimens to *Operculina* cf. *O. panamensis* (Cushman). If this identification was correct, an Oligocene age for this locality would be indicated.

Cole (in Weyl, 1957, p. 135) identified from samples collected near the Damas river (loc. 2) *Camerina macgillavryi* M. G. Rutten. At that time Cole considered that this species was an upper Eocene marker. From another sample collected near Jicotea Cole identified 3 undoubted upper Eocene species of larger Foraminifera.

This study was undertaken as part of a program made possible by a scholarship from the Institute of International Education and the Costa Rican government. Dr. W. Storrs Cole of Cornell University directed the study. I express my appreciation and thanks to him for his time and efforts.

LOCALITIES

Upper Cretaceous

Loc. 1. Near the village of Murcielago; red, massive coraline limestone.

1A. El Viejo farm in the Tempisque valley; in addition to larger Foraminifera *Nerinea epelys* and rudists occur (W. P. Woodring, personal communication).

Middle Eocene

2. Damas Cavern near the Damas 7 kms. northwest of the Damas farm of the Cia. Bananera; massive, cream-colored limestone.

Upper Eocene

3. Junquillal Bay; gray limestone with abundant calcareous algae.

4. Punta Serrucho near the mouth of the Naranjo River 10 kms. southwest of Puerto Quepos; mottled, cream-colored limestone.

5. El Cajon gorge of the Terraba River about 15 kms. from the village of Palmar; massive, dense, poorly bedded, cream to

FIG. 1—Map of Costa Rica, showing sample location.

gray limestone with some calcareous algae.

6. Outcrops on each side of the Parrita River at San Marcos de Tarrazu on the Carmen Mora farm; gray limestone containing masses of calcareous algae and abundant large microspheric specimens of *Lepidocyclina* (*Eulepidina*) *chaperi* Lem. and R. Douvillé.
7. Las Animas village 3 kms. northeast of Turrialba; cream-colored limestone with calcareous algae.
8. Below the bridge across the Reventazon River between the villages of Chitaria and Peralta; fossiliferous conglomerate.
9. Punta Pelada 3 kms. northeast of Guiones Point on the Pacific Coast, gray to white sandy limestone.

FAUNAS AND CORRELATION

The distribution of the species at the various localities is shown in Table 1.

Brönnimann (1957, p. 590) has stated that *Pseudorbitoides israelskyi* "appears to be diagnostic of beds of Taylor age (Upper Santonian and Campanian) in Texas and Mississippi, probably also at its type locality in Louisiana." Therefore, the localities (loc. 1 and 1A) may be correlated with the Taylor of the Gulf Coast of the United States.

Camerina macgillavryi M. G. Rutten (1935, p. 530), the only species found in the single middle Eocene sample (loc. 2) with

TABLE 1—DISTRIBUTION OF THE SPECIES

Species	Upper Cretaceous		Middle Eocene	Upper Eocene					Upper Oligocene	
	1	1A	2	3	4	5	6	7	8	9
Pseudorbitoides israelskyi Vaughan and Cole	c	c								
Sulcoperculina dickersoni (O. K. Palmer)	r	r								
Camerina macgillavryi M. G. Rutten			a							
Asterocyclina asterisca (Guppy)				r	a		c	a		
marianensis (Cushman)				r				r		
minima (Cushman)						c		c		
**Camerina floridensis* (Heilprin)				r	r					
striatoreticulata (L. Rutten)				a	r		r			
Fabiania cassis (Oppenheim)				r	c	r				
Heterostegina ocalana Cushman				r		r				
Lepidocyclina (*Pliolepidina*) *macdonaldi* Cushman				c	c					
pustulosa H. Douvillé				r	c	a	c	c		
**(Eulepidina*) *chaperi* Lem. and R. Douvillé				c			a	c		
Pseudophragmina (*Proporocyclina*) *flintensis* (Cushman)					c					
**Camerina dia* (Cole and Ponton)									r	r
Heterostegina antillea Cushman										c
Lepidocyclina (*Eulepidina*) *undosa* Cushman									a	
vaughani Cushman										a
Miogypsina (*Miogypsina*) *antillea* (Cushman)									c	c

* See: Cole (1960*a* and 1960*b*) for generic and subgeneric classification.
r = rare; c = common; a = abundant.

the exception of a few fragments of a small *Asterocyclina* sp., was described from Cuba from strata assigned to the upper Eocene. Later, Butterlin (1959, pl. 14, fig. 54) illustrated specimens which are without doubt *C. macgillavryi* from the middle Eocene of Haiti. Cole (1958*b*, p. 265) considered that this species seemingly is a diagnostic one for the middle Eocene.

All of the upper Eocene localities (locs. 3–7) are correlated with the Gatuncillo formation of Panama and the San Fernando formation of Trinidad, a correlation which Cole (1957, p. 749) had made previously.

The Oligocene localities (locs. 8,9) are correlated with the upper Oligocene part of the Caimito formation and the Bohio formation of the Panama Canal Zone and vicinity. Inasmuch as *Miogypsina* (*Miogypsina*) occurs at both localities, they are assigned to the *Miogypsina* (*Miogypsina*) subzone of the *Eulepidina* zone of the Caribbean area (Cole, 1958*a*, p. 220).

Miogypsina (*Miogypsina*) *tani* Drooger (= *M.* (*M.*) *antilla* Cushman) occurs at its type locality in Costa Rica in association with *Lepidocyclina* (*Eulepidina*) *undosa* Cushman and *Camerina dia* (Cole and Ponton). In Panama (Cole, 1957, p. 314) as well as in Costa Rica *M.* (*M.*) *antillea* occurs with *Lepidocyclina* (*Eulepidina*) *vaughani* Cushman. In Panama (Cole, 1953*a*, p. 6) and in Antigua (Vaughan, 1933, p. 33) *L.* (*E.*) *vaughani* occurs with *L.* (*E.*) *undosa*. Therefore, *M.* (*M.*) *antillea* is a species of the *Eulepidina* zone of the American Oligocene.

Akers and Drooger (1957, p. 658) placed *M.* (*M.*) *tani* (= *M.* (*M.*) *antillea*) stratigraphically above the zone of *L.* (*E.*) *undosa* in the western and central Gulf Coast of the United States. The data presented here suggest that either *M.* (*M.*) *antillea* has a more extensive stratigraphic range than suggested by Akers and Drooger, or the assumption made by them is incorrect.

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JOURNAL OF PALEONTOLOGY, V. 35, NO. 3, P. 502–504, PL. 71, MAY, 1961

MUSCLE ATTACHMENT IMPRESSIONS IN A CRETACEOUS AMMONITE[1]

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ABSTRACT—Muscle attachment impressions in an Upper Cretaceous ammonite, *Diplomoceras notabile*, Whiteaves consist of a pair of bean-shaped retractor muscle impressions on the dorsal (antisiphonal) side, and a single, nearly round, impression on the venter, the origin and function of which is not known.

The muscular attachment system in *D. notabile* appears to differ from the typical nautiloid attachment system in lacking a continuous annular elevation and in having a single ventral attachment impression.

INTRODUCTION

MUSCLE attachment impressions are extremely rare in ammonites and few reliable illustrations of such features are available. However, during the process of describing a large Upper Cretaceous ammonite fauna from the Matanuska formation, south central Alaska, several specimens of *Diplomoceras notabile* Whiteaves were found in which the muscle attachment impressions are extremely well preserved.

Because of their rarity, little attention has been paid to ammonite muscle attachments; the most comprehensive treatment is that by Crick (1898) who described the attachment impressions in a number of Mesozoic ammonites. Many of Crick's illustrations are rather vague and their validity has never been completely accepted. Spath (1919, p. 178) states that "Mr. Crick thought that the traces of muscular attachment of the Ammonoid animal to its shell afforded important characters for the purposes of classification; but both on account of the comparative scarcity and the indefinite nature of these impressions they have not proved of value yet in the classification of Ammonites." Similar expressions of doubt are also found in the recent Ammonoidea volume of the Treatise on Invertebrate Paleontology (Arkell, 1957, p. L81).

The situation is somewhat better with respect to muscle attachment impression in nautiloids, where, according to Sweet (1959, p. 295) 31 genera have been found to exhibit such impressions. Mutvei (1957, p. 219–254) and Sweet (1959, p. 293–304) have summarized the literature dealing with nautiloid muscle attachment impressions, and both have illustrated several specimens which clearly show the nature of the attachments in both recent *Nautilus* and fossil nautiloids.

It is, therefore, of considerable interest to compare well preserved muscle attachment impressions of an ammonite with those of nautiloids. The ammonite material described herein consists of specimens of the late Campanian or early Maestrichtian ammonite *Diplomoceras notabile* Whiteaves (1903, p. 335) obtained from the Matanuska formation, Talkeetna Mountains, south-central Alaska. Four specimens were found in which the muscle attachment impressions could be observed. Three of these specimens were collected on Mazuma Creek at Latitude 62°4′50″ N., Longitude 147°50′00″ W. (U. S. Geol. Survey Loc. M562, collectors, D. L. Jones and A. Grantz, 1959). The fourth specimen was obtained nearby at Latitude 62°04′50.5″ N. and Longitude 147°50′07″ W. (U. S. Geol. Survey Mesozoic Loc. 24860, collectors A. Grantz and L. Fay, 1953).

MUSCLE ATTACHMENT IMPRESSIONS IN *DIPLOMOCERAS NOTABILE*

Three muscle attachment impressions are observed on the internal mold; two paired impressions are present on the dorsal (antisiphonal) side, and a single, nearly round impression is present on the ventral (siphonal) side. The dorsal impressions consist of two bean-shaped depressions which measure about 14 mm. in a transverse direction and about 9 mm. in a longitudinal direction.

[1] Publication authorized by the Director, U. S. Geological Survey.

They are located about 10 mm. below (adorally) the last septum of the septate portion of the shell. The outer margin of each bean-shaped impression consists of a narrow, incised line, bounded within by a slight elevation. The attachment surface is covered by faint, longitudinal striations which are more prominent on the anterior (adoral) side than on the posterior (adapical) side. A shallow furrow or constriction lies between the muscle attachment impressions and the last septum. This constriction becomes much deeper on the ventral side.

Other faint striations are present on the dorsal surface between the bean-shaped attachment impressions and the last septum. Presumably, these represent attachment impressions of other muscles.

The ventral muscle attachment impression is located below (adorally) the dorsal impressions, but on the same oblique rib or ribs. This impression is nearly circular and measures about 6 mm. in a transverse direction and about 5 mm. in a longitudinal direction. It is situated about 20 mm. below the last septum of the septate portion, from which it is separated by a deep constriction. This attachment has only been observed on two specimens; the other two specimens being too deeply weathered on the ventral surface to permit its observation.

Other features present on the ventral surface consist of faint striations which converge on a point formed by the intersection of a medioventral line and the last septum. This marks the approximate position of the intersection of the septum and the siphuncle.

COMPARISON WITH NAUTILOID MUSCLE ATTACHMENT IMPRESSIONS

Mutvei (1957) and Sweet (1959) have shown in considerable detail the nature of the muscular attachment impressions in nautiloids so only a brief summary of their observations is necessary here.

Nautiloids possess three main muscle attachment areas, all of which are in the posterior (adapical) part of the body chamber (Mutvei's term "domiciliary cavity" seems to have little advantage over the simpler term). This region in which all three attachments occur is slightly elevated, and is called the "annulus" or "annular elevation" (Mutvei, 1957). Longitudinal mantle muscles are attached in a single, narrow band along the adoral margin of this elevation; the powerful retractor muscles, or "shell" muscles are attached in two broad, paired areas just posterior to the mantle attachment. Other body, or subepithelial, muscles are attached in a narrow band at the posterior end of the chamber near its junction with the last septum. Thus, the nautiloid system of muscular attachments consists of two continuous bands for attachment of the body and mantle muscles and two discrete spots, or paired areas, for the attachment of the retractor muscles. As Mutvei and Sweet (1959, p. 310) have pointed out, the retractor muscle impressions may be located either ventrally (ventromyarian), dorsally (dorsomyarian), or laterally (pleuromyarian).

The two large, dorsal, paired muscle impressions in *Diplomoceras notabile* probably served as attachments for the retractor muscles similar to those in nautiloids. The function of the third muscle attached to the venter is not known, and a corresponding analog does not seem to be present in nautiloids. Also, a raised area similar to the annular elevation of nautiloids was not observed in *D. notabile* although it would seem that some comparable structure should be present for the attachment of the mantle and subepithelial muscles.

CONCLUSIONS

It would perhaps be unwise to speculate too deeply on the significance of the muscular attachment impressions of *D. notabile*, particularly as this species is heteromorphic and may have had a quite different mode of living than normally coiled ammonites. No positive conclusions can yet be drawn and full evaluation of Ammonoid attachment musculature must await the description of these features in many more species.

In summary, *D. notabile* differs from typical nautiloids in having three points of muscle attachment, rather than a pair and two bands. The statement that "ammonoids seem invariably to be dorsomyarian, regardless of the adaptational plasticity—" (Sweet, 1959, p. 302) cannot be fully accepted until the significance of the ventral muscle attachment is determined.

Another point worth commenting upon is

that some of Crick's (1898) illustrated muscle scars are based on reliable observations. The specimens figured by Crick on plate 17, figures 6–13, and plate 19, figures 11–14, have dorsal muscle attachment impressions nearly identical to those of *D. notabile*.

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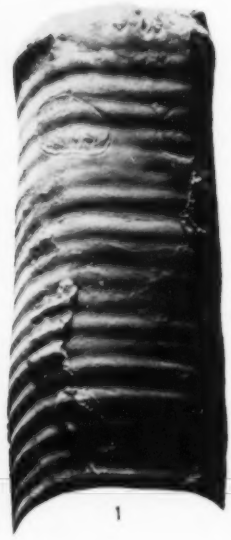
MANUSCRIPT RECEIVED APRIL 10, 1960

EXPLANATION OF PLATE 71

FIGS. *1–4*—*Diplomoceras notabile* Whiteaves, USNM 130867, from U.S.G.S. Mes. loc. M562. *1,2*, dorsal views showing bean-shaped, paired, retractor muscle attachment impressions, ×1; *3*, ventral view showing single, rounded muscle attachment impression, ×1; *4*, complete specimen, side view; arrows show position of dorsal and ventral muscle attachment impressions and position of last septum (S). ×½.



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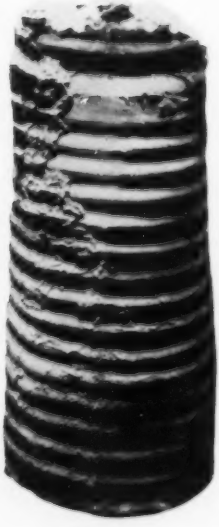

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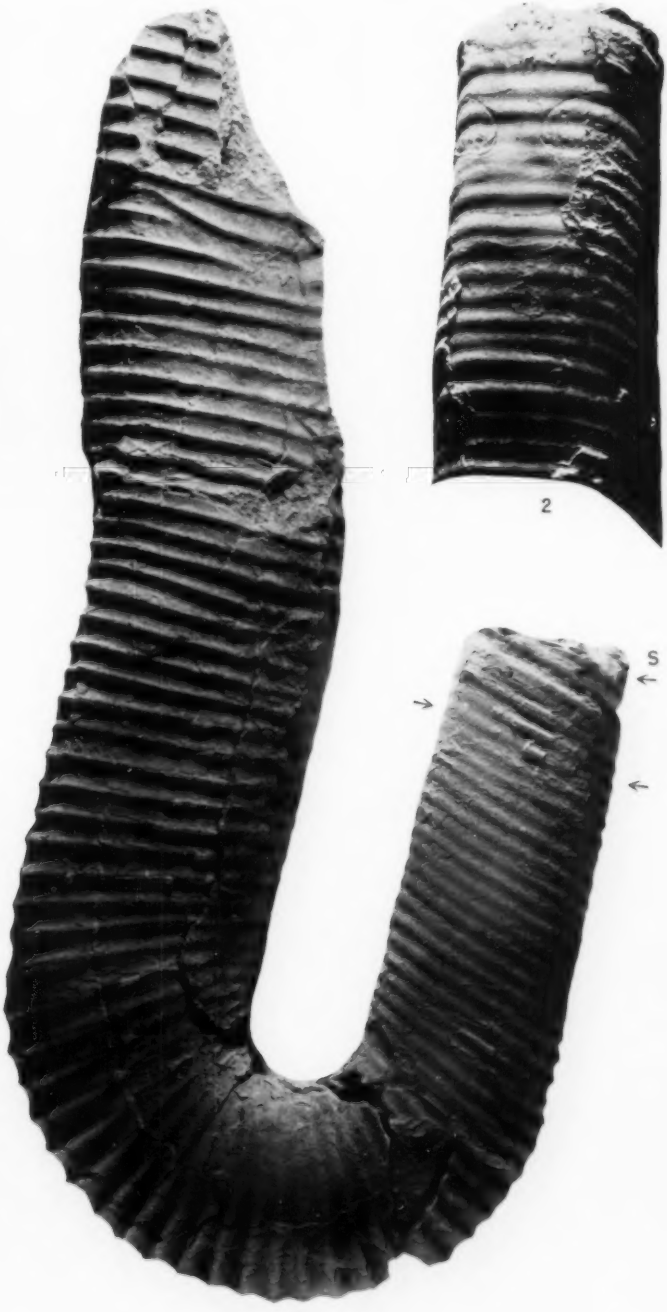

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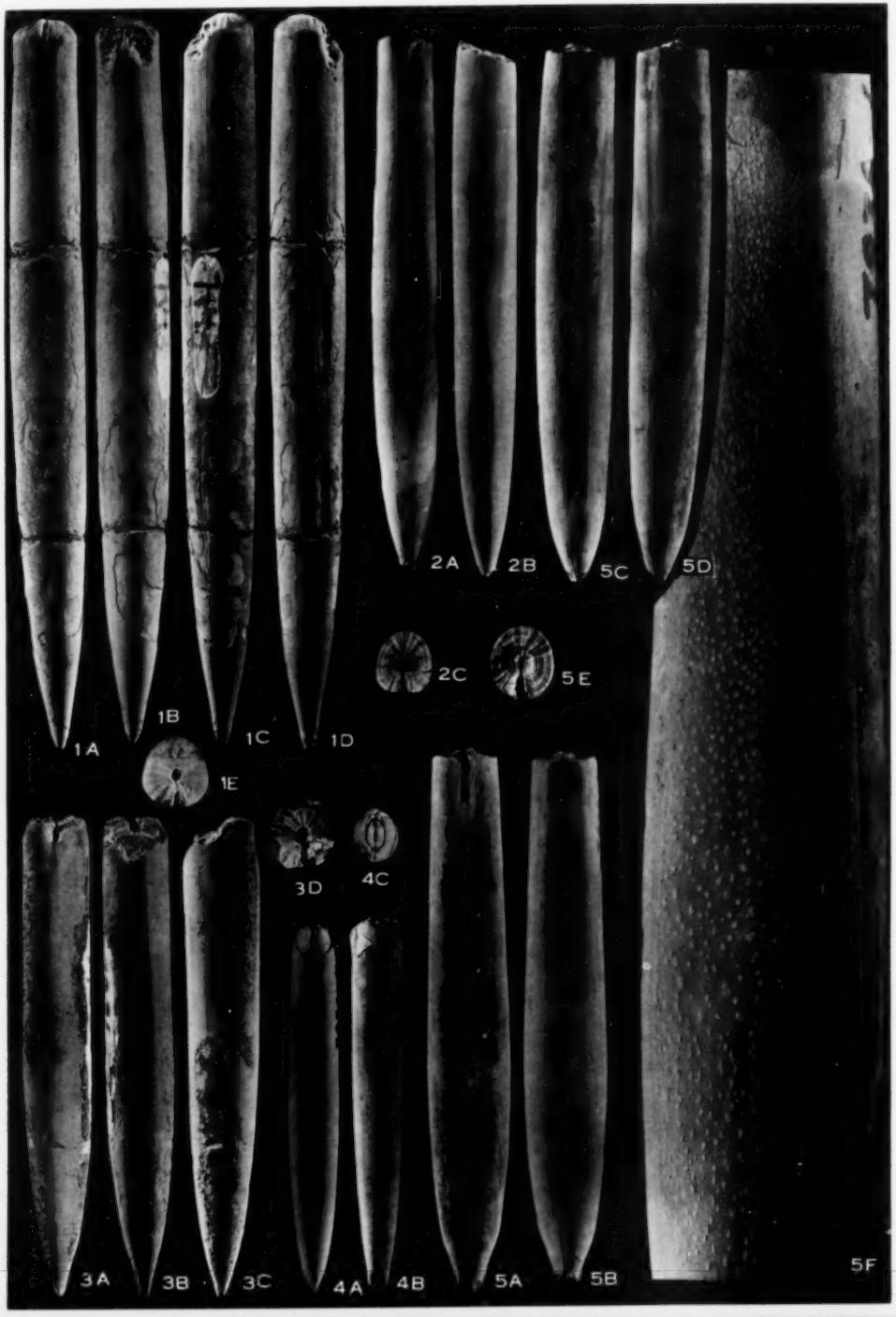
1A
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JOURNAL OF PALEONTOLOGY, V. 35, NO. 3, P. 505–531, PL. 72, 6 TEXT-FIGS., MAY, 1961

ACTINOCAMAX FROM THE UPPER CRETACEOUS BENTON AND NIOBRARA FORMATIONS OF KANSAS[1]

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(*Abstract will be found on next page*)

INTRODUCTION AND ACKNOWLEDGEMENTS

MILLER (1957) has recently described and figured some belemnites from the Niobrara formation of Kansas. These he has somewhat tentatively identified as *Belemnitella praecursor* Stolley, a representative of which species was described and figured (Jeletzky, 1955) from the western interior of the United States shortly before the appearance of Miller's paper. Jeletzky (1955) inferred from the somewhat incomplete label and the lithology of the rock filling out the alveolar cavity of the guard that this speci-

[1] Published by Permission of the Director, Geological Survey of Canada, Ottawa, Canada.

EXPLANATION OF PLATE 72

(All figures natural size unless otherwise indicated)

FIG. *1*—*Actinocamax manitobensis* (Whiteaves, 1889) var. *kansanus* n. var. Holotype. Benton group below Fort Hays limestone of the Niobrara and presumably from the Fairport chalky shale of the Carlile shale. Upper Turonian (lower part?).

Dutch Hallow in Rush Co., Kansas; near the Ellis Co. line; presented to the Fort Hays College by A. N. Schuttle, Ellis, Kansas. Fort Hays College Cat. No. 7143.

1A, Central view; *1B*, dorsal view; *1C*, left lateral view; *1D*, right lateral view; *1E*, view of the alveolar end from above; ventral side is below.

2—*Actinocamax manitobensis* (Whiteaves, 1889) f. typ. This specimen is transitional to *A. manitobensis* var. *lawrencii* Jeletzky, 1950 in the structure of its pseudoalveolus.

According to the museum label it was "picked up by George F. Sternberg in Gove or Logan Co., in the Niobrara Cretaceous chalk, exact locality unknown." Presumed to have come from rocks of the Upper Turonian (lower part?) stage. Fort Hays College, Cat. No. 7936–2.

2A, ventral view; *2B*, right lateral view; *2C*, view of the alveolar end from above. Note the depressed character of pseudoalveolus and the almost complete absence of the edge within it.

3—*Actinocamax walkeri* n. sp. Holotype. Niobrara Cretaceous chalk, Gove or Logan Co., Kansas. Picked up by George F. Sternberg. Exact locality and year not known. The age can range from the uppermost Turonian to the Lower Campanian but is more likely to be Coniacian. Fort Hays College, Cat. No. 7936-3.

3A. ventral view; *3B*, dorsal view; *3C*, left lateral view; *3D*, view of the alveolar end from above.

4—*Actinocamax walkeri* n. sp. Same horizon and locality as for the specimen No. 7936-3. Fort Hays College, Cat. No. 7936-5.

4A, ventral view; *4B*, left lateral view; *4C*, view of the alveolar end from above; note the strong lateral compression of the alveolar end, which was obviously caused by the pressure of sediment after the guard was buried.

5—*Actinocamax sternbergi* n. sp. Holotype. Niobrara Cretaceous chalk, Gove or Logan Co., Kansas. Exact locality not known. Picked up by George F. Sternberg, exact year not known. Cat. No. 7936-1. The age can range from the uppermost Turonian to the Lower Campanian but is more likely Coniacian or lowermost Santonian.

5A, ventral view; *5B*, dorsal view; *5C*, right lateral view; *5D*, left lateral view; *5E*, view of the alveolar end from above; *5F*, view of the middle part of the dorsal side of the guard ×3 to show the details of its granulation and of the double dorsolateral furrows (*see* right side of the picture).

ABSTRACT—The following forms of *Actinocamax* are described and figured from the Upper Cretaceous Benton and Niobrara formations of Kansas: *A. manitobensis* (Whiteaves) f. typ., *A. manitobensis* var. *kansanus* n. var. *A.* cf. *manitobensis* var. *spicularis* n. var., *A. sternbergi* n. sp., *A. Walkeri* n. sp., *Actinocamax* sp. aff. *A. laevigatus* Arkhangelsky, *Actinocamax* sp. indet. *A.* (? aff. *A. manitobensis* Whiteaves). The belemnite material studied includes all Niobrara belemnites recently described by Miller (1957) as *Belemnitella praecursor* Stolley. These belemnites are revised and placed in the genus *Actinocamax* s. str.

The described *Actinocamax* forms from Kansas range from the late Turonian to the late Santonian or early Campanian age. The Coniacian to (?) early Campanian *Actinocamax* forms are closely allied to the West Greenland *Actinocamax* faunas recently described by Birkelund (1956). The late Turonian *Actinocamax* fauna is identical with the *A. manitobensis* fauna from Manitoba. The previously informally described Canadian *Actinocamax* sp. aff. *A. strehlensis* Fritsch and Schloenbach is revised in connection with the description of the Kansas *Actinocamax;* it is assigned to the species *A. manitobensis* as its new variety (var. *spicularis* n. var.).

The alveolar and apical ends of several *Actinocamax* forms from Kansas are deformed so as to indicate that they were sufficiently soft and pliable to be squashed or bent by the pressure of sediment after the burial of the guards.

men of *Belemnitella praecursor* was collected in the yellow chalk member of the upper Niobrara formation of Kansas.

Miller (1957, p. 908,911) has stressed that his belemnite specimens differed from *Belemnitella praecursor* Stolley var. *media* Jeletzky in the complete absence of the alveolar cavity; he has, however, ascribed this distinction to the subsequent loss of the alveolar part of the guard by all of his specimens. The published figures of these specimens (Miller, 1957, p. 909, text-figs. 1A–1D) showed, however, this interpretation to be in conflict with the characteristic weathering shapes of their alveolar ends. This weathering was rather suggestive of these specimens belonging to the genus *Actinocamax* Miller 1826 s. str. as defined by Jeletzky (1950, p. 3). To verify this interpretation the writer has loaned all of the belemnites studied by Miller (1957) from Mr. George F. Sternberg, Curator of the Fort Hays Kansas State College. The results of their study are presented below.

The writer is grateful to Mr. George F. Sternberg, Curator of the Fort Hays State College, Hays, Kansas for lending him the above mentioned belemnite material, providing him with valuable information about their localities and stratigraphic positions within the Upper Cretaceous sequence of Kansas, and granting permission to publish descriptions and photographs of them. Mr. Myrl V. Walker of the same College and Dr. Halsey W. Miller, Jr. of the Geology Department of University of Arizona, Tucson have kindly provided the writer with valuable additional stratigraphical information about some of the described belemnites.

PALAEONTOLOGICAL DESCRIPTIONS

The collection studied consists of nine belemnite specimens, most of which are well preserved and more or less complete. Eight of these specimens display characteristic appearance of the alveolar ends diagnostic of the genus *Actinocamax* Miller s. str. (Jeletzky, 1950, p. 3) and so belong to this genus rather than to the genus *Belemnitella* d'Orbigny emend. Jeletzky, 1941. The ninth specimen is a fragment lacking alveolar and apical ends. The characteristic outline and cross-section of this fragment permit, nevertheless, its tentative identification as *Actinocamax* cf. *manitobensis* var. *spicularis* nov. var.

Genus ACTINOCAMAX Miller 1826 s. str.
ACTINOCAMAX MANITOBENSIS (Whiteaves, 1889) *s. l.*

Material studied: Three of the here described guards are referable to the Canadian *Actinocamax* species—*A. manitobensis* (Whiteaves, 1889) s. lato; one of them is referable to the typical variety of this polytypic species in the sense of Jeletzky (1950). A new variety of the species is proposed herewith to accomodate another Kansas specimen and its study threw a new light upon the range of morphological variation of *A. manitobensis*. The morphology of *A. manitobensis* var. *kansanus* n. var. is, indeed, transitional between that of *A. manitobensis* var. *trehernensis* Jel. and that of the hitherto

insufficiently understood *Actinocamax* sp. aff. *A. strehlensis* Fritsch and Schloenbach. This, and the occurrence in the Kansas collection of a fragment apparently referable to *A.* sp. aff. *A. strehlensis*, has necessitated the revision of the last mentioned form and its inclusion in *Actinocamax manitobensis* as its morphologically extreme variety *A. manitobensis* var. *spicularis* n. var.

The recurrence of *A. manitobensis* and its varieties in Kansas is of a considerable palaeogeographical and biochronological interest, particularly in view of the great paucity of the Upper Cretaceous rocks of Kansas in reliable index fossils.

Diagnosis: The previously given diagnosis of *A. manitobensis s. l.* (Jeletzky, 1950, p. 4) must be amended as follows in order to accomodate *A. manitobensis* var. *kansanus* n. var. and *A. manitobensis* var. *spicularis* n. var.: Guard large, long, either subcylindrical to fairly lanceolate in ventral and lateral aspects or tapering gradually and evenly all the way apicad from its alveolar end in lateral aspect; reasonably stout to very slender; ventral surface more or less flattened except in the laterally compressed alveolar region; a feeble to pronounced ventral furrow occurs immediately below the alveolar rim; alveolar end is ovate in cross-section; the shape of alveolar end varies from a shallow pseudoalveolus 4–7 mm. deep to a low, protruding, more or less regularly rounded cone with the embryonic bulb at its top; when well preserved, the surface of the guard bears weak to pronounced longitudinal striae.

ACTINOCAMAX MANITOBENSIS
(Whiteaves) 1889 f. typ.
Pl. 72, figs. 2A–2C;

Belemnitella manitobensis Whiteaves, 1889, p. 189 (no figure)
Actinocamax manitobensis Jeletzky, 1950, p. 4–10, text-fig. 1, pl. 1, figs. 1–5; pl. 11, fig. 4.
Belemnitella praecursor Miller, Jr., 1957, Text-figs. A1, 1D.

Material Studied. One of the Kansas guards studied belongs to typical form of *A. manitobensis;* it is reproduced on pl. 72, figs. 2a–2c.

Description. The only Kansas guard known is large (87.5 mm. long) and slender, with the elongation ratio of about 7.9 times; it is fairly lanceolate in ventral aspect and only slightly lanceolate, almost subcylindrical, in lateral aspect; the maximum lateral diameter of 11.2 mm. is situated somewhat below the middle of the guard and about 35 mm. above its apical end; the maximum dorso-ventral diameter of 11.1 mm. is situated only about 22 mm. below the alveolar end of the guard; the mid-section of the ventral surface of this latter is, however, strongly corroded throughout and this diameter could, therefore, have originally been situated further apicad at about the middle of the guard.

In ventral aspect the guard tapers evenly orad from the level of the maximum diameter to a point 5 mm. below the alveolar end where a slight contraction of its profile occurs; therefrom it expands slightly and evenly to the outer rim of the depressed pseudoalveolus where the lateral diameter of the guard is 9.3 mm.

Apicad the guard tapers equally gradually and evenly in ventral aspect from the level of the maximum diameter to the level some 12 mm. above the apical end; further down the tapering increases progressively to a point some 2 mm. above the apical end of the guard resulting in the convex and somewhat obtuse appearance of the guard's flanks in this interval; the basal 2 mm. of the guard are shaped in the form of an ill-defined spine superimposed on a somewhat rounded but nevertheless narrow base; the spine is broken off some 2–3 mm. above its tip, judging by the fact that the fracture is about 3 mm. in diameter.

The almost subcylindrical lateral outline of the guard persists from the alveolar end to the level some 17–18 mm. above the apex; further apicad the guard tapers gradually and almost evenly to the apical end; the average dorso-ventral apical angle is 28–29°; only a suggestion of the rounded apex and spine, such as are visible in ventral aspect, can be observed in the lateral aspect.

The lateral profile of the guard is somewhat asymmetrical near the alveolar end; the ventral side tapers somewhat towards the outer edge of pseudoalveolus within the upper 8 mm., and the dorsal side continues to extend more or less in the same direction as before within this interval.

The guard is distinctly compressed later-

ally at the alveolar edge. There its dorso-ventral diameter is 10.3 mm. as compared to the lateral diameter of only 9.3 mm.; the lateral compression persists throughout the upper third of the guard, becoming weaker and weaker apicad until the diameters become about equal some 32 mm. below the alveolar end. Dorso-ventral compression prevails further apicad with the dorso-ventral diameter being only 10.5 mm. at the level of the maximum lateral diameter about 35 mm. above the apex. The ventral side of the guard is noticeably flattened already at the alveolar edge (pl. 72, fig. 2C); this flattening increases gradually apicad until it reaches the maximum value at about the level of the maximum lateral diameter where the ventral surface is pronouncedly flattened; it decreases somewhat again within the apical fifth of the guard.

The dorsal side of the guard is somewhat flattened throughout its posterior three-fifths, although much less than is the ventral side in the same interval; this results in the asymmetrically oval cross-section of the guard throughout the posterior half. The flattening decreases rapidly above the guard's middle and is absent throughout the anterior third of the same where the dorsal side of the guard protrudes somewhat between the anteriorly converging dorso-lateral depressions.

The surface of the guard appears to be smooth with only a few short and weak, oblique or longitudinal striae visible under favourable light conditions here and there on the posterior half; better expressed, but nevertheless fine and weak longitudinal furrows cover most of the guard's surface between the apex and the level 10 to 12 mm. above the latter (pl. 72, figs. 2A–2B).

Single lateral furrows could not be observed with certainty.

Double dorso-lateral furrows first appear in the somewhat dorso-lateral position about 8 mm. above the apex on both sides of the guard and extend straight, parallel, and strictly longitudinally all over the posterior half; these furrows are 0.3–0.4 mm. wide and are separated from each other by a 0.5 mm. wide interspace; near the point of the first appearance the furrows are difficult to distinguish from the adjacent, closely spaced, longitudinal furrows. Some 42 mm. above the apex the double dorso-lateral furrows enter the dorso-lateral depressions, which begin at about that level; they disappear almost immediately thereafter.

The longitudinal, dorso-lateral depressions are very shallow and devoid of any inner relief; their width is about 2 mm. at the posterior end but they expand to about 3 mm. at the outer edge of pseudoalveolus. The more clearly defined dorsal margins of the depressions converge gradually towards the alveolar end of the guard while the almost imperceptible ventral margins run virtually longitudinally in the same direction. The dorsal field of the guard becomes more and more narrow, and at the same time increasingly elevated, orad between the dorsal margins of the dorsolateral depressions.

The truncated alveolar end is "hoof-like" but rounded in cross-section, with the ventral side forming a straight line, except for the rounded corners; it is depressed throughout and forms a shallow pseudoalveolus, which is 4.5 to 5.0 mm. deep at its center. The outer edge of the alveolar end is tilted towards the dorsal side of the guard in lateral aspect at about 20° (pl. 72, fig. 2B). The walls of pseudoalveolus have a markedly convex profile; they are only slightly depressed throughout the outer third of pseudoalveolus but the inward dip of their walls increases gradually towards its center and reaches some 40° in the central third of pseudoalveolus. The boundary between both parts of pseudoalveolus is not sharp; the profile of pseudoalveolus is rather similar to that of the specimens of *Actinocamax manitobensis* figured by Jeletzky (1950, pl. I, figs 3,5; text-fig. 1).

The surface of pseudoalveolus exposes the edges of concentric growth-layers of the guard; these latter display a characteristic lamellar and radial pattern and radial cross-ridges typical of *Actinocamax* in general and of *A. manitobensis* in particular (Jeletzky, 1950, p. 6; this paper pl. 72, fig. 2C).

In the specimen here discussed there are 15 radial ridges of unequal prominence and size crossing the surface of depressed pseudoalveolus; most of them are situated on its dorsal side (pl. 72, fig. 2C).

The embryonic bulb is visible at the bottom of the deepest, central part of pseudo-

alveolus; it is about 1 mm. wide but its bottom is partly covered by the remaining rock. A deeply incised furrow, broadly gaping in its outer half, crosses the ventral side of pseudoalveolus (pl. 72, fig. 2C); in the central, steep part of pseudoalveolus this furrow begins 1.0 to 1.5 mm. above the embryonic bulb; its walls remain in contact throughout the inner part of pseudoalveolus; there the furrow obviously represents the well preserved, lowermost part of the ventral fissure originally present in all *Actinocamax* (Jeletzky, 1950, p. 7–8). The gaping outer (upper) part of the furrow cuts through the upper part of the wall of pseudoalveolus and forms a 4 mm. long, gaping, irregularly curved fissure on the ventral surface of the guard just below the edge of pseudoalveolus (pl. 72, fig. 2A). This gaping ventral fissure is obviously caused by the weathering and decay of the substance of the guard around the originally present ventral furrow and along the bottom of the ventral fissure adjoining this latter (Jeletzky, 1950, p. 7–8).

Remarks. Although well within the known range of variation of the typical form of *A. manitobensis*, the here described guard is obviously transitional between this form and *A. manitobensis* var. *lawrencii* in its relatively deep alveolus with the only weakly developed edge between its outer and inner parts (Jeletzky, 1950, p. 6), as well as in its strongly developed although short ventral fissure. In above features the Kansas guard virtually duplicates the Canadian guard reproduced by Jeletzky, 1950 on pl. 1, figs. 3a–3c, text-fig. 1. These two guards are also extremely similar in their ventrally lanceolate and laterally subcylindrical shape.

The Kansas guard is much smaller and more slender than the majority of the Canadian guards. Only the young guard of *A. manitobensis* reproduced by Jeletzky on pl. I, figs. 1a–1c is smaller than the Kansas guard. The Kansas guard is therefore apparently a half grown representative of the species. This assumption is further strengthened by its comparison with the corresponding growth-lines of the adult Canadian specimen reproduced by Jeletzky (1950, p. 4, text-fig. 2).

Locality, Stratigraphic Position and Age. According to the written communication of Mr. George F. Sternberg, the guard here described was: "picked up by George F. Sternberg in Gove or Logan Co., in the Niobrara Cretaceous chalk, exact locality and year not known."

In the western interior of Canada, however, *A. manitobensis* (Whiteaves, 1889) and all its varieties appear to be restricted to the late, but not the latest, Turonian. As shown by Jeletzky (1960) this species is only known from the regional *Ostrea lugubris* zone. This Canadian zone corresponds to part or all of the following late Turonian zones of the western interior of the United States (ascending order):

(1) *Prionocyclus* (*Collignoniceras*) *hyatti* and *Scaphites carlilensis*.

(2) *Prionocyclus* (*Collignoniceras*) *macombi* and *Scaphites warreni*.

(3) *Prionocyclus* (*Prionocyclus*) *wyomingensis* and *Scaphites ferronensis*.

(4) *Scaphites nigricollensis*, *Prionocyclus reesidei*, and

(5) *Scaphites corvensis*.

All of the above zones of the western interior of the United States are older than the oldest zone known in the Niobrara formation—that of *Scaphites preventricosus* and *Inoceramus deformis*. The Niobrara formational assignment of the Kansas specimen of *A. manitobensis* f. typ. is, therefore, in conflict with the now known time-range of the species. This discrepancy can be explained in several ways:

(1) The Niobrara of Kansas may include rocks older than those of the *Scaphites preventricosus* and *Inoceramus deformis* zone;

(2) *Actinocamax manitobensis* et var. may have a longer time-range than hitherto known; and

(3) The Kansas specimen here described was mislabelled and was actually found in rocks older than those of the Niobrara formation.

The explanation (2) is quite improbable. *Scaphites preventricosus* and *Inoceramus depressus* zone, which was assumed to be of the latest Turonian age by Jeletzky (1960), contains, indeed, an entirely different *Actinocamax* fauna in U.S.A. (Montana) as well as in Canada. This fauna shall be described elsewhere.

The explanation (1) is possible, as the fauna of the lower Niobrara of Kansas is still imperfectly known. The writer does not

know, however, of any supporting paleontological evidence in the American literature.

Explanation (3) is favoured by the writer as the Kansas specimen of *A. manitobensis* var. *kansanus* described below was collected from the Carlile shale, and most likely from the Fairport chalky member of this formation. The Kansas fragment of *Actinocamax* cf. *manitobensis* var. *spicularis*, although from an uncertain horizon and locality, may also have been collected from below the Fort Hays limestone of the Niobrara formation (*see* below).

It is, therefore, suggested tentatively that the Kansas guard of *A. manitobensis* f. typ. here discussed was actually collected in the Fairport chalky shale member of the Carlile shale. It is hoped that this assumption shall be checked upon by American colleagues working in Kansas.

Actinocamax manitobensis var. kansanus n. var.

Pl. 72, Figs. 1A–1E, Text-figs. 1a–1b

Diagnosis. Guard very slender and long; its elongation ratio is about 10 times; slightly lanceolate in ventral and in lateral aspect and tapers gently and gradually toward the apical and alveolar ends from the level of maximum diameters; apical end very acute, with the dorso-ventral apical angle of only 23°; alveolar end protrudes and forms a low, rounded mound slanted irregularly toward the dorsal side of the guard.

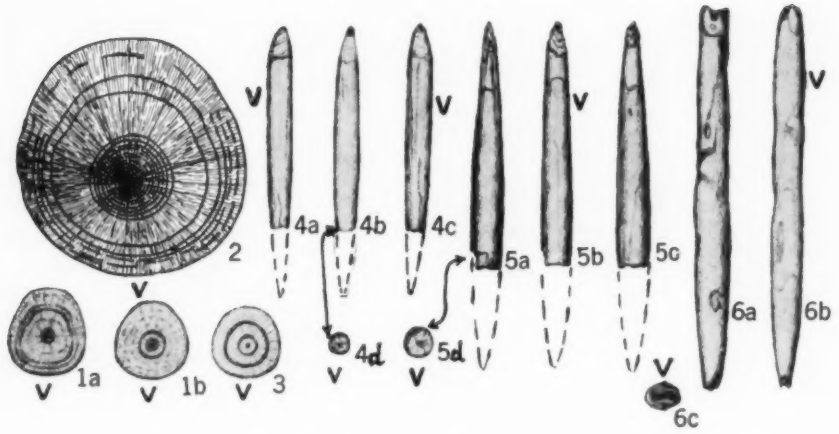
Type Specimen. The only known specimen of *A. manitobensis* var. *kansanus* (pl. 72, fig. 1A–1E) is its holotype by monotypy; it is preserved in the collections of the Fort Hays College, Hays, Kansas, Cat. No. 7143.

Description. Guard is very slender and long (length 125 mm.) with the elongation ratio of about 9.8 times; it is rather large and slightly lanceolate in ventral as well as in lateral aspect. Critical dimensions and ratios are given in Table 1. From the level of the maximum diameters, which are situated 47–51 mm. below the rim of the alveolar end, the guard tapers very gently and evenly orad in both aspects all the way to the rim of the alveolar end; apicad the guard tapers almost imperceptibly in lateral and in ventral aspects from the level of maximum diameters to that 45 mm. above the apex; further apicad the tapering increases progressively but gradually all the way towards the apex; this results in the somewhat convex outline of the apical third of the guard in lateral and ventral aspects. The apical end is very acute and nonmucronated; the apical angle measures only 23° in the dorso-ventral plane. The lateral profile of the guard is slightly asymmetrical (pl. 72, fig. 1C-1D) its dorsal outline being gently convex while the ventral outline is almost straight, except near the apical and alveolar ends of the guard. The apical end of the guard is slightly displaced toward its dorsal side.

The surface of the guard is mostly almost smooth; it only shows weak longitudinal striae in several places, particularly in the apical third of the guard. In one or two places, however, the upper layer of the guard is peeled off exposing the next older layer, which is covered by strong and closely spaced but thin longitudinal furrows (pl. 72, fig. 1A). This suggests that the almost smooth appearance of the remaining part of the guard's surface is caused by its imperfect preservation.

The ventral side of the guard is somewhat flattened throughout the middle three-fifths of its length (Text-figs. 1a,1b), the flattening almost disappears closer to the alveolar and apical ends of the guard. The dorsal side distinctly protrudes throughout the alveolar half of the guard between the dorso-lateral depressions, which converge gradually toward the alveolar end of the guard; it is only slightly flattened throughout this interval. The alveolar end is ovate in cross-section, the dorso-ventral diameter being greater than the lateral diameter; the latter is situated closer to the ventral side of the guard (pl. 72, fig. 1E). The lateral compression of the alveolar end gradually decreases apicad and becomes replaced by the moderate dorso-ventral compression of the guard already in its upper third; further apicad this dorso-ventral compression becomes more pronounced in the middle two-fifths of the guard; it decreases again in the apical fifth of the same.

The alveolar end of the guard protrudes somewhat above the alveolar edge of the same; it forms a more or less regularly rounded, low mound that bears a 2 mm. wide, round, and steeply conical hole at its



EXPLANATION OF TEXT-FIGURES

TEXT-FIGS. *1a–1b*. *Actinocamax manitobensis* (Whiteaves, 1889) var. *kansanus* n. var. Two cross-sections of the holotype figured in pl. 72, figs. 1A–1E; *1a*, cross-section at the level about 37 mm. below the alveolar end (at the upper fracture visible in pl. 72, figs. 1A–1D); *1b*, cross-section at the level about 36 mm. above the apical end (at the lower fracture visible in pl. 72, figs. 1A–1D). both cross-sections ×1.

TEXT-FIG. *2*. *Actinocamax* cf. *A. manitobensis* (Whiteaves, 1889) var. *spicularis* n. var. Kansas. Locality and formation uncertain. The specimen has been presumably collected in the Benton formation below the Fort Hays limestone in Upper Turonian (lower part?) beds. Fort Hays College, Cat No. 10367. Cross-section of the anterior end of the fragment ×3.

TEXT-FIG. *3*. *Actinocamax walkeri*. n. sp. Cross-section of the holotype figured on pl. 72, figs. 3A–3D at the level about 26 mm. above the apical end (at the fracture visible in pl. 72, figs. 3A–3C) ×1.

TEXT-FIGS, *4a–4d*. *Actinocamax* sp. aff. *A. laevigatus* Arkhangelsky 1912. Niobrara formation. Smoky Hill chalk member. Trego County. Kansas. Probably not more than 50 feet above the top of Fort Hays limestone. ?Upper Santonian. Collected by Mr. Orrin D. Oppliger. Fort Hays College Cat. No. 10368. *4a*, right lateral view; *4b*, ventral view; *4c*, left lateral view; *4d*, cross-section of the guard at its broken off posterior end. The missing apical part of the specimen restored from the general outline of its preserved part. All figures ×1.

TEXT-FIGS. *5a–5d*. *Actinocamax* sp. aff. *A. laevigatus* Arkhangelsky 1912. Niobrara Cretaceous chalk, Gove or Logan Co., Kansas. Picked up by George F. Sternberg. Exact locality and year not known. Probably was collected at about the same level within the Niobrara formation as the specimen No. 10368. ?Upper Santonian. Fort Hays College Cat. No. 8126. *5a*, dorsal view; *5b* left lateral view; *5c*, ventral view; *5d*, cross-section of the guard at its broken off posterior end. The missing apical part of the specimen restored from the general outline of its preserved part. All figures ×1.

TEXT-FIGS. *6a–6c*. *Actinocamax* sp. indet. A. (?aff. *A. manitobensis* Whiteaves, 1889). Niobrara Cretaceous chalk. Gove or Logan Co., Kansas. Picked up by George F. Sternberg. Exact locality and year not known. The age of the specimen can range from the latest Turonian to the early Campanian but it was more likely collected from the uppermost Turonian or Coniacian rocks. Fort Hays College Cat. No. 7936–4. *6a*, ventral view; *6b*, left lateral view. Note that the alveolar end of the guard is strongly squashed in dorso-ventral direction (compare also text-fig. *6c*); *6c*, view of the alveolar end from above. All figures ×1.

The ventral side of the guard is marked "v" in all figures.

middle (top); the latter is 1.5–2.0 mm. deep, with the embryonic bulb situated at its bottom. The protruding, truncated surface of the alveolar end shows a typical" actinocamaxoid" sculpture, such as occurs in other varieties of *A. manitobensis* (Jeletzky, 1950, p. 6). The dorsal third of the protruding alveolar end is destroyed by weathering; two irregular hollows with an irregular ridge between them occur there (pl. 72, fig. 1B). The ventral side of the protruding alveolar end bears a fissure, which cuts through the

TABLE 1—CRITICAL DIMENSIONS AND RATIOS OF THE COMPLETE GUARDS OF INVESTIGATED *Actinocamax* FORMS

Specimens	A Overall length	B Maximum dorso-ventral diameter (height above apex in mm. in brackets)	Ratio B/A	C Maximum lateral diameter (height above apex in mm. in brackets)	Ratio C/A	Diameters at the alveolar end: Dorso-ventral	Diameters at the alveolar end: Lateral	Apical angle (dorso-ventral)	Depth of pseudo-alveolus	Length of ventral fissure and (or) furrow
Actinocamax walkeri n. sp.										
No. 7936-3 (Holotype)	78.6	12.9 (69.0 above)	0.16	11.8 approx. value only (37.5 above)	0.15	12.6	11.2	31°–32°	—	6.0–6.5 mm. (approx.)
No. 7936-5	61.5	8.8 (43.6 above)	0.14	8.5 (32.0 above)	0.14	alveolar end laterally squashed		20°–21° (approx.)	—	3.5 mm. (approx.)
Actinocamax manitobensis (Whiteaves 1889) f. typ.										
No. 7936-2	87.5	11.1 (65.5 above)	0.13	11.2 (35.0 above)	0.13	10.3	9.3	28°–29°	4.5–5.0	4.0 mm.
Actinocamax manitobensis (Whiteaves 1889) var. *kansanus* n. var.										
No. 7143 (Holotype)	125.0	12.7 (78.0 above)	0.10	12.7 (74.0 above)	0.10	11.9	10.9	23°	—	24–25 mm.
Actinocamax sternbergi n. sp.										
No. 7936-1 (Holotype)	89.0	13.2 mm. (49 mm. above)	0.15	13.9 (33 mm. above)	0.15	12.0	10.9	37°–38°	—	10.7 mm.

ventral wall of the above described conical hole and connects it with the pronounced, much wider, deeply incised furrow occurring on the ventral side of the guard just below the alveolar rim. This incised ventral furrow continues for about 5 mm. apicad from the alveolar rim; further apicad it changes into a shallow furrow with a rounded profile, which continues for another 19–20 mm. apicad gradually becoming less conspicuous and finally disappearing completely at the end of this interval (pl. 72, fig. 1A). The above discussed ventral fissure apparently begins quite close to the embryonic bulb within the conical hole crowning the protruding alveolar end. The observed relationships are, thus, much the same as those in *Actinocamax* sp. aff. *A. strehlensis* (Jeletzky, 1950, p. 14).

Short, single lateral furrows are faintly visible under favourable light conditions on both sides of the guard in its alveolar quarter; they begin close to the flattened ventral surface of the guard at their posterior ends and run obliquely orad gradually approaching the dorso-lateral depressions. These single lateral furrows are 10 to 15 mm. long and seem to end blindly on both ends; they are not visible on the photographs.

Double dorso-lateral furrows and longitudinal depressions harbouring the former over the anterior half of the guard are rather strongly developed. The double dorso-lateral furrows begin close to the apical end of the guard in the middle of its flanks; they become more distinct further orad and gradually shift into their normal dorso-lateral position in this direction; the furrows are about 0.5 mm. wide and are separated from each other by a similarly wide elevated interval throughout the apical half of the guard; they are not accompanied by any depressions throughout this interval, except for an irregularly shaped longitudinal depression on the right side of the guard occuring between the levels 38 to 48 mm. above the apex (pl. 72, fig. 1D); this depression is believed to be pathological in nature. The double dorso-lateral furrows run an essentially straight course throughout their observed length. Some 55 mm. above the apex they become indistinct and enter the bottom of the dorso-lateral depressions, which become apparent on the guard's flanks at about that level. Dorso-lateral depressions are some 2–3 mm. wide and about 1 mm. deep at the point of their first appearance; they gradually become wider toward the alveolar end of the guard, becoming at the same time more shallow and converging gradually toward the borders of the guard's dorsal side in the same direction; they are 5 to 7 mm. wide near the outer edge of the alveolar end. Indistinct longitudinal ridges and secondary longitudinal depressions occur within dorso-lateral depressions on the anterior two-fifths of the guard; it was not possible, however, to connect these with the double dorso-lateral furrows, which become lost within their lower part.

The character of the ontogenetic development could not be observed on the only specimen studied.

Remarks.—*A. manitobensis* var. *kansanus* n. var. is of considerable taxonomical interest in being morphologically transitional between *A. manitobensis* var. *trehernensis* and *Actinocamax manitobensis* var. *spicularis* n. var. This indicates that the latter form previously described as *Actinocamax* sp. aff. *A. strehlensis* Fritsch et Schloenbach is but an extreme morphological variety of the here described species (*see* below).

Stratigraphic Position, Locality and Age. The label of the only known specimen of *A. manitobensis* var. *kansanus* reads: "Dutch Hallow in Rush Co., Kansas; near Ellis Co. line; presented by A. N. Schuttle, Ellis, Kansas."

According to Mr. Myrl V. Walker (letter of January 24th, 1958) the specimen #7143: "came from below the Fort Hays limestone and probably from the Fairport chalky shale of the Carlile shale. This is well down in the old "Benton" series. The Fairport chalky shale contains thin chalk beds similar in appearance to the Smoky Hill chalk." Dr. Halsey W. Miller, Jr. adds (letter of January 15th, 1958) that: "the specimen #7143 is definitely from the Benton and that its locality is situated near the Greenhorn-Graneros outcrops."

This stratigraphic placement of specimen #7143 is in a perfect agreement with the known time range of *A. manitobensis* f. typ. et var. in Canada (*see* above). It is assumed, therefore, that *A. manitobensis* var. *kansanus* is a geologically contemporary morphological variety of that species rather

than a closely related but independent palaeontological species (evolutionary stage) occurring in older or younger Turonian rocks of Kansas.

Origin of Name.—From the State of Kansas where its holotype and the only known specimen was found.

ACTINOCAMAX MANITOBENSIS var. SPICULARIS n. var.
Text-fig. 2

?*Actinocamax plenus* Geinitz, 1872–75, p. 180, pl. 31, figs. 13,14 non 15

Actinocamax sp. aff. *A. strehlensis* Jeletzky, 1950, p. 12–17, text-fig. 2, pl. III, figs 1,4,5.

Diagnosis.—*See* Jeletzky, 1950, p. 12.

Type Specimen.—The specimen G.S.C. #9670 figured by Jeletzky (1950, p. 12, pl. III, fig. 4) was already sighted as the provisional type specimen of this informally described *Actinocamax* form; it is now formally selected as the holotype of this form following its naming as a new morphological variety of *Actinocamax manitobensis* (Whiteaves, 1889) s. lato in this paper.

Description.—*See* Jeletzky, 1950, p. 12.

The only Kansas specimen tentatively referred to *A. manitobensis* var. *spicularis* n. var. is a fragment, which represents most of the posterior half of the guard and some of its anterior part; it is 47 mm. long with both ends broken off and polished; at the anterior end of the fragment the dorso-ventral diameter is 12.1 mm. and the lateral diameter is 11.1 mm.; at the posterior end of the fragment the dorso-ventral diameter is 7.5 mm. and the lateral diameter is 8.0 mm.; the fragment tapers markedly but evenly all the way apicad in ventral as well as in lateral aspect, which is characteristic of *Actinocamax manitobensis* var. *spicularis* n. var.

The surface of the fragment appears to be completely smooth; this is, however, obviously due to its being strongly corroded. The dorso-lateral depressions are but faintly visible near the anterior end of the fragment. The growth-lines visible in the fracture of the upper end of the fragment (text-fig. 2) give a much better idea about the original cross-section of the guard than the outline of its surface; this cross-section has a rounded trapezoidal shape and is characterized by the somewhat flattened dorsal side protruding between fairly strongly incised dorso-lateral depressions; the ventral side is more strongly flattened; the lateral diameter of the outermost growth-line is 7.8 mm. and the dorso-ventral diameter is 7.2 mm. A still younger cross-section with the lateral diameter of 4.1 mm. and dorso-ventral diameter of 3.8 mm. is more regularly ovoid in outline with only weakly expressed dorso-lateral depressions; it still has the flattened ventral side and marked dorso-ventral compression, however.

Affinities and Differences.—The writer's doubts about the specific independence of *Actinocamax* sp. aff. *A. strehlensis* (Jeletzky, 1950, p. 14) were confirmed by the discovery of *A. manitobensis* var. *kansanus* in the Carlile shale (?Fairport chalky shale) of Kansas. The latter variety is morphologically transitional between *Actinocamax* sp. aff. *A. strehlensis* and *A. manitobensis* var. *trehernensis*. *Actinocamax* sp. aff. *A. strehlensis* is, therefore, now considered to be only an extreme morphological variety of *A. manitobensis* s. l. for which the name *A. manitobensis* var. *spicularis* n. var. is proposed herewith.

The *Actinocamax* forms from the Upper Turonian rocks of Strehlen (Czechoslovakia) described and figured by Geinitz (1872–75, p. 180, pl. 31, figs. 13,14) are tentatively identified as the European representatives of *A. manitobensis* var. *spicularis;* they apparently only differ from the Canadian representatives of this variety in their smaller size.

The legitimate cotypes of *Actinocamax strehlensis* Fritsch and Schloenbach emend. Stolley, 1916 figured by Fritsch and Schloenbach (1872, p. 18, pl. 16, figs. 10–12) differ from the Canadian and ?European representatives of *A. manitobensis* var. *spicularis* in their much shorter and stouter guard, depressed shape of the alveolar end, and in pronouncedly lanceolate shape of the guard in ventral and lateral aspects; the two forms are here considered to be specifically distinct.

Actinocamax manitobensis var. *spicularis* differs from *A. intermedius* Arkhangelsky, 1912 s. str. (Jeletzky, 1949, p. 421) in the same features as from *A. strehlensis* Fr. et. Schloenb. em. Stoll. It is, furthermore, probable that this upper Turonian form is

synonymous with *A. strehlensis* Fr. et. Schloenb. em. Stoll. The close affinity of *A. intermedius* and *A. strehlensis* was recently confirmed by Soviet workers (Naidin, 1956, p. 21).

The close affinity of *A. manitobensis* var. *spicularis* with *A. primus* Arkhangelsky, 1912 has already been stressed (Jeletzky, 1950, p. 15–16). The typical form of the latter species—*A. primus* var. *primus* Birkelund, 1957—differs from juvenile and adult representatives of *A. manitobensis* var. *spicularis* in:

(1) Slightly lanceolate to subcylindrical outline of the guard in lateral aspect;

(2) Shorter and sturdier guard; and

(3) Generally smaller dimensions.

These morphological differences are well illustrated by the specimens of *A. primus* var. *primus* Birkelund reproduced by Arkhangelsky (1912, pl. X, figs. 1–5), Jeletzky (1948, text-fig. 1) and Birkelund (1957, pl. 1, figs. 1,4).

The extreme slender form of *A. primus*—*A. primus* var. *elongata* Arkhangelsky, 1912—often has a guard that is just as slender and long as that of *A. manitobensis* var. *spicularis;* its guard tapers, furthermore, gently and evenly apicad in lateral aspect from the alveolar rim to the posterior third of its length. Such forms of *A. primus* var. *elongata* were figured by Birkelund (1957, pl. 1, figs. 2,3); they can only be distinguished from *A. manitobensis* var. *spicularis* in the constantly smaller size of their guards. All larger representatives of *A. primus* known to the writer differ, indeed, from *A. manitobensis* var. *spicularis* in above listed morphological features (1) to (3).

Taking into the consideration that *A. primus* var. *elongata* and *A. manitobensis* var. *spicularis* are the extreme morphological varieties of the generally speaking easily distinguishable *Actinocamax* forms occurring in beds of a different geological age, their close morphological similarity is obviously due to homoeomorphy.

Locality, Stratigraphic Horizon and Age.—According to the museum records the only known Kansas fragment of *A.* cf. *manitobensis* var. *spicularis*, which is preserved in the Fort Hays College, Hays, Kansas, Cat. No. #10367, was found in a miscellaneous collection of fossils received from the widow of the late Mr. Fay van Wormer. The horizon is uncertain. According to Mr. Myrl V. Walker (letter of January 24th, 1958) this fragment: "may have also come from below the Fort Hays limestone. It came to the museum from a private collector who collected considerable material from the old 'Benton' series."

In Canada *A. manitobensis* var. *spicularis* is, as far as now known, confined to the Assiniboine member of the Favel formation in Manitoba and Saskatchewan. In Alberta it was found in the regional *Ostrea lugubris* zone of the Cardium (= Bighorn) formation. In northeastern British Columbia it occurs in the Tuskoola sandstones of the Pine River area (Jeletzky, 1960). All beds containing *A. manitobensis* var. *spicularis* in Canada were found to be of the late, but not the latest, Turonian age; they appear to be contemporary with the late Turonian Strehlen beds of Czechoslovakia, which carry *Actinocamax* forms apparently indistinguishable from *A. manitobensis* var. *spicularis* (Geinitz, 1872–75, p. 180, pl. 31, figs. 13,14).

The above described fragment of *A.* cf. *manitobensis* var. *spicularis* from Kansas is assumed to have been collected from the part of Carlile shale equivalent to the Canadian *Ostrea lugubris* zone.

ACTINOCAMAX STERNBERGI n. sp.
Pl. 72, figs. 5A–5F

Belemnitella praecursor Miller, Jr., 1957, Text-figs. 1B,1C.

Diagnosis.—Guard large and moderately stout, slightly lanceolate in lateral aspect and feebly lanceolate in ventral aspect; entire surface covered with closely spaced, small granules, which generally show no definite arrangement; the alveolar end flatly truncated but with a protruding low, rounded mound in the middle; a small, rounded hole with the protoconch at its bottom occurs at the top of this mound. A gaping ventral fissure runs across the ventral side of the alveolar end beginning only about 0.5 mm. above the protoconch; it extends for 8 mm. below the rim of the alveolar end on the ventral side of the guard. Double dorso-lateral furrows are well defined, shallow, flat-bottomed and unusually wide (0.8–1.2 mm.); they are separated from

each other by well defined, unusually wide (0.9–1.1 mm.) interspaces.

Type Specimen.—The only known specimen of *Actinocamax sternbergi* is its holotype by monotypy. This specimen is figured on pl. 72, figs. 5A–5F; it is preserved in the Fort Hays College, Hays, Kansas, Cat. No. 7936-1.

Although generally opposed to the formal naming of unique specimens, the writer has decided to make an exception in this particular instance because of the excellent preservation of this interesting *Actinocamax* form and its sharp distinction in all essential taxonomical features from all other hitherto described *Actinocamax* species. The informally described East Greenland form—*Actinocamax* aff. *groenlandicus* Birkelund—is the only exception. This form (Birkelund, 1956, p. 11–13, pl. 1, figs. 4a–4d) may be a geographical subspecies or a morphological variety of *Actinocamax sternbergi*.

Description.—The guard is large (89 mm. long) and moderately stout, with the elongation ratio of about 6.7 times; slightly lanceolate in lateral aspect and weakly lanceolate in ventral aspect; the maximum dorso-ventral diameter of 13.2 mm. is situated only about 40 mm. below the alveolar end while the maximum lateral diameter of 13.9 mm. lies much lower, about 33 mm. above the apical end of the guard.

In the ventral aspect the guard tapers evenly and gradually orad all the way from the level of the maximum diameter to the alveolar end; the lateral diameter decreases to 10.9 mm. at the alveolar rim; below the maximum lateral diameter the guard's contraction in the ventral aspect is slight at first but increases gradually further down to the level about 8 mm. above the apex; this results in the gently convex outline of the guard throughout this interval; yet further apicad the contraction increases abruptly to about 38°, which value is maintained to the very apex of the guard; this causes the straight, conical ventral outline of the guard closely above the apex (pl. 72, figs. 5A,5B).

In lateral aspect the guard tapers almost imperceptibly orad from the level of the maximum diameter to the level of the base of the alveolar fissure; higher up the contraction increases only slightly on the dorsal side of the guard; on the ventral side, however, it increases somewhat more markedly; this results in the slightly asymmetrical lateral profile of the guard, which is further stressed by the slight displacement of the apical end of the same toward the dorsal side discussed below (pl. 72, figs. 5C,5D). The dorso-ventral diameter decreases to 12.0 mm. at the alveolar rim. Apicad the guard tapers almost imperceptibly and evenly from the level of its maximum dorso-ventral diameter to the level about 8 mm. above the apex; further apicad the contraction increases abruptly to about 37–38° also in the lateral aspect (pl. 72, figs. 5C,5D). This angle of contraction is then maintained to the apex, it results in the same straight and conical outline of this part of the guard as in dorsal and ventral aspects. It seems likely, however, that the value of the above contraction was increased by the dorso-ventral compression of the apical end of the guard described below.

The apical end of the guard is slightly displaced toward the dorsal side; it is about 3.5 mm. wide at the place of the break off; the latter is level and perpendicular to the guard's longitudinal axis; no traces of the rounded apex or of the mucro are preserved.

For 2.5–3.0 mm. above the tip, the apical end of the guard is peculiarly compressed dorso-ventrally so as to suggest that its substance was still capable of plastic deformation under the pressure of sediment after the guard's burial (pl. 72, figs. 5A,5D). Three short longitudinal wrinkles accompanied by cracks occur on the right side of the deformed part of the guard (pl. 72, fig. 5C); these have obviously resulted from the deformation of the guard. The deformation itself was apparently caused by the incomplete calcification of the guard in *Actinocamax sternbergi*. This phenomenon shall be discussed more fully below in connection with the description of similar plastic deformations of parts of the guards observed in *Actinocamax walkeri* nov. sp.

The guard is markedly compressed laterally at the alveolar end; the lateral compression there is accompanied by a considerable flattening of the lateral sides of the guard at that level and further down throughout the anterior third; this lateral compression and flattening gradually de-

creases apicad and finally disappears some 35 mm. below the alveolar end of the guard where the dorso-lateral diameter is already 13.2 mm. and the lateral diameter is 13.1 mm. Further apicad the guard is markedly compressed dorso-ventrally throughout; at the level of the maximum lateral diameter of 13.9 (33 mm. above apex) the dorso-ventral diameter is only 12.6 mm. and the cross-section has the shape of a symmetrically flattened oval; ventral and dorsal sides of the guard are also markedly flattened in its posterior two-thirds, the former being somewhat more flattened. This flattening gradually decreases orad from the level of the guard's maximum lateral diameter. In the case of the dorsal side it almost disappears some 22 mm. below the alveolar end of the guard; some flattening persists, however, all the way to the rim of the alveolar end (pl. 72, fig. 5E) where it is reflected in the somewhat angular cross-section of this latter. The ventral side remains somewhat stronger flattened throughout this interval.

The dorsal side of the guard protrudes somewhat between the gradually converging orad dorso-lateral depressions throughout the anterior quarter of the guard (pl. 72, fig. 5B).

The entire surface of the guard is ornamented by the densely spaced, small granulae, mostly ranging from 0.15 to 0.5 mm. in diameter. The granulae can be rounded, oval, square, or irregularly elongated in cross-section; the interspaces between them vary from one to five diameters of the granulae (pl. 72, fig. 5F). Although they are disorderly arranged over most of the guard's surface, the granulae may form closely spaced, longitudinal rows along the margins of double dorso-lateral furrows and dorso-lateral depressions (*see* below); they are, furthermore, often absent, or rare and subdued, within these furrows and depressions (pl. 72, figs. 5A–5D,5F); on the right side of the guard (pl. 72, fig. 5c) they form, finally, several ill-defined rows on the posterior third. These rows run obliquely toward the guard's ventral side from the more ventrally situated of the double dorso-lateral furrows, with which they form an acute angle of less than 30°. These rows of granulae seem to represent the modified vascular imprints, which so often occur on the corresponding parts of the flanks of other *Actinocamax* species.

The granulae are smaller and more densely crowded all over the anterior half of the guard as compared with the posterior half of same; they become more sparse, subdued, and are commonly only barely perceptible, on the flanks of the guard in the interval between the apex and the level some 10–11 mm. above this latter.

A few faint, mostly short and slightly wavering, longitudinal striae and furrows occur on the dorsal and ventral sides of the guard in the anterior quarter of the same.

The single, lateral furrows are weakly developed; that on the left side of the guard (pl. 72, fig. 5D) persists over its upper third to the very alveolar end; it begins near the ventral side of the guard and runs obliquely and with a noticeable wavering to the point of the alveolar rim situated almost in the middle of the guard's flank. Only a 11–12 mm. long section of the single lateral furrow is visible in the upper third of the right side of the guard (pl. 72, fig. 5C); it runs longitudinally throughout this interval.

The double dorso-lateral furrows begin about 10 mm. above the apex on both sides of the guard; above the point of their first appearance they are sharply defined and are engraved directly in the rounded flanks of the guard throughout the posterior half of same. The double dorso-lateral furrows appear in the somewhat dorso-lateral position; on the left side of the guard (pl. 72, fig. 5D) they extend slightly obliquely, gradually approaching the dorsal side of the guard; on the right side of the guard, however, they extend strictly longitudinally (pl. 72, fig. 5C). These furrows are unusually wide (0.8 to 1.2 mm.), shallow, flat-bottomed, and are separated from each other by unusually wide (1.0 to 1.1 mm.), slightly elevated interspaces covered with granules, which are sometimes (pl. 72, fig. 5D) arranged in rows along their edges. Whenever present, this arrangement of granules is apt to create the impression of two elevated lines occurring along the edges of interspaces between double dorso-lateral furrows and separated by an additional furrow from each other.

The longitudinal dorso-lateral depressions, which harbour the above discussed

double dorso-lateral furrows throughout the anterior half of the guard, begin about 45 mm. above the apex and continue orad to the alveolar rim of the guard; they are about 2.5 mm. wide at the point of their first appearance and gradually widen orad to become 4.5 to 5.0 mm. wide just below the rim of the guard's alveolar end (pl. 72, figs. 5C,5D,5F).

The ventral margins of the longitudinal depressions are almost imperceptible even in the favourable light, while their dorsal margins are sharply defined. Pronounced but round-bottomed, 1.5 mm. wide and 0.75 mm. deep longitudinal furrows run just inside dorsal margins of the depressions; they are the direct continuations of the more dorsal furrows of the above described double dorso-lateral furrows (pl. 72, figs. 5C,5D,5F). Indistinct, broadly and gently rising, longitudinal elevations occupy the middle parts of the longitudinal depressions. Barely perceptible longitudinal furrows separate these elevations from the ventral margins of the same depressions; these furrows seem to represent the orad continuations of the more ventral ones of the above discussed double dorso-lateral furrows but it was not possible to trace the connection between them across the mid-section of the guard.

The so called dorsal field of the guard is limited by the dorsal margins of the longitudinal depressions and by the more dorsal ones of the double dorso-lateral furrows (pl. 72, figs. 5B, 5F); it is about 9.6 mm. wide at the point of the first appearance of the double dorso-lateral furrows but becomes 11.7 mm. wide at the level 39 mm. above the apex because of the slight divergence of the furrows in the orad direction within this interval; higher up first the furrows and then the margins of the longitudinal depressions converge evenly and gradually orad all the way to the alveolar end of the guard, where the dorsal field becomes only 7.0 mm. wide. As the dorsal field of the guard becomes more narrow orad, it becomes progressively more elevated and more regularly rounded.

The truncated alveolar end of the guard is regularly oval in cross-section; the longer axis runs in dorso-ventral direction (pl. 72, fig. 5E). Only the central portion of the alveolar end, which is 4.0–4.5 mm. wide and more or less circular in outline, protrudes slightly and forms a low cone with the rounded top; a small, about 1.5 mm. wide and about 2.0 mm. deep, steeply dipping and conical, round hole occurs atop of this cone, exactly in the center of the truncated alveolar end; the protoconch occurs at the bottom of this hole. The rest of the truncated alveolar end is virtually level with its outer edges; its surface is, however, slightly inclined toward the dorsal side of the guard.

The alveolar end of the guard exposes the edges of the growth layers throughout; these form concentric rings. The surface of the truncated alveolar end of the guard is intersected by about 14 radial ridges of different height and width (pl. 72, fig. 5E). Most of the ridges do not cross the central elevated part of the alveolar end of the guard.

The ventral side of the truncated alveolar end is crossed by a fissure, which begins within the above mentioned round hole only about 0.5 mm. above the protoconch; this fissure cuts through the protruding part of the alveolar end of the guard; the walls of the fissure are only 0.25 mm. from each other within this interval. The fissure becomes gaping throughout the flat part of the alveolar end, its walls being about 1.4 mm. apart within this interval; simultaneously the bottom of the fissure plunges obliquely apicad; it forms an angle of 15°–18° with the ventral surface of the guard but its course is not straight but slightly concave. The similarity of the outline of the bottom of ventral fissure of *Actinocamax sternbergi* with that of *Actinocamax* aff. *groenlandicus* Birkelund (1956, pl. 1, fig. 4c) is striking.

The ventral fissure reaches the ventral surface of the guard about 8.7 mm. below the rim of the alveolar end and continues for another 2 mm. apicad in the form of a shallow, 2 mm. wide ventral furrow (pl. 72, fig. 5A), which then disappears. It is believed that the above described, gaping fissure represents the secondarily deepened and broadened ventral furrow (Jeletzky, 1950, p. 7–8), except where it cuts through the protruding part of the alveolar end; it is also possible, of course, that the gaping part of the fissure represents the secondary deepening and broadening of the original "splitting surface" such as was described by

Jeletzky (1946, p. 100–101, text-fig. 3) in some other *Actinocamax* species.

The ontogeny of *A. sternbergi* could not be studied in the only specimen available.

Affinities and Differences.—*A. sternbergi* belongs to the so called granulated stock of *A. verus* Miller, 1826. The taxonomic value of granulation was stressed by Jeletzky (1950, p. 4). Birkelund's (1956, p. 11) remark that this feature may not always be diagnostic on the specific level appears to be correct, however; this definitely puts in doubt the previously assumed taxonomical value of granulation within the genus *Actinocamax* s. str.

Actinocamax aff. *groenlandicus* Birkelund (1956, p. 11–13, pl. 1, figs. 4a–4d) is undoubtedly the closest known ally of *A. sternbergi;* it agrees with the latter species in most of the essential morphological characters. *A. sternbergi* only differs from the East Greenland form in:

(1) Much more extensive granulation with more numerous and more closely spaced granules;

(2) Slightly lanceolate outline of the guard in lateral aspect;

(3) Slightly less protruding and somewhat differently shaped alveolar end;

(4) Stronger development of the double dorso-lateral furrows and longitudinal depressions;

(5) Presence of the single lateral furrows; and

(6) Much greater width and different appearance of the double dorso-lateral furrows.

Distinctions (1) to (5) seem to be taxonomically unimportant on the specific level, especially as the only known guard of *A.* aff. *groenlandicus* was found in the basal Upper Campanian conglomerate apparently reworked from older Upper Cretaceous rocks (Birkelund, 1956, p. 11–12). It could, therefore, have easily been much more extensively granulated originally, with more strongly developed double dorso-lateral furrows and longitudinal depressions; also the absence of single lateral furrows in *A.* aff. *groenlandicus* could easily be due to their subsequent abrasion.

It is, therefore, possible that *A.* aff. *groenlandicus* is conspecific with *A. sternbergi*, being either the morphological variety or the geographical subspecies of the latter species. The distinction (6) in the width and general appearance of the double dorso-lateral furrows is, however, believed to be taxonomically significant on specific level and it is for that reason that the writer has refused to place *A.* aff. *groenlandicus* in the synonymy of *A. sternbergi*, at least for the time being.

Actinocamax groenlandicus Birkelund (1956, p. 5–11, pl. 1, figs. 1a–1c,2,3a–3c) differs from *A. sternbergi* in:

(1) Shallow, depressed pseudoalveolus;

(2) Much less extensive granulation;

(3) Presence of extensive and strongly expressed longitudinal striation;

(4) Longer ventral fissure;

(5) Greater slenderness, longer and more acute apical end, and at first subcylindrical and then slowly tapering lateral outline of the guard.

Morphological distinctions (1), (2), (3), and (4) appear to be taxonomically significant on specific level. Taken together with the less significant distinctions in the shape of the guard, they are considered to be ample for the specific separation of the two forms concerned.

All other hitherto described North American *Actinocamax* forms differ sharply from *A. sternbergi* already in the total lack of granulation. They cannot be confused with it and so shall not be further discussed here.

Among the Eurasian *Actinocamax* species, *Actinocamax westfalicus* Schlüter differs from *A. sternbergi* in:

(1) Weak development or total lack of granulation;

(2) Much shorter and stouter guard;

(3) Development of vascular imprints and striae;

(4) Much smaller size; and

(5) Several other less significant morphological features.

These distinctions are ample for the specific separation of these two forms.

Although somewhat similar to *A. sternbergi* in their granulated surface, all known representatives of the genus *Gonioteuthis* Bayle, 1878 differ so much from the North American form in all other important morphological features that they shall not be further discussed here.

Actinocamax bohemicus Stolley, 1916

(Fritsch and Schloenbach, 1872, pl. 16, fig. 17) is, like *A. sternbergi*, granulated almost throughout; it differs, however, from the Kansas species in:

(1) Granules forming patterns of the corrugated transverse lines;

(2) More distinctly triangular cross-section of the alveolar end;

(3) Moderately protruding, rounded alveolar end of the guard; and

(4) Even, gradual tapering of the guard from the alveolar end to the apical quarter in ventral aspect. There is little doubt about the specific independence of these two forms.

Actinocamax verus Miller, 1826 and its varieties are all granulated throughout or almost throughout; their granules form, however, patterns of corrugated, transverse lines unlike the granules of *A. sternbergi*. All these forms are, furthermore, so unlike the Kansas species in their markedly fusiform shape, mostly strongly protruding alveolar end, small size and greater stoutness that even their closer affinity with *A. sternbergi* appears improbable, not to mention the specific identity.

Actinocamax padebornensis Schlüter, 1894 is similar to *A. sternbergi* in being granulated, large and relatively stout. This form was not figured, however, and is based on a single fragment of the guard. No detailed comparison with *A. sternbergi* is, therefore, possible at present.

Actinocamax depressus Andree var. *ornata* Moberg (1885) is the only granulated representative of the Eurasian group of species typified by *A. mammillatus* Nilsson. It differs strongly, however, from *A. sternbergi* in the depressed pseudoalveolus, strongly fusiform shape of the guard in ventral as well as in lateral aspects, much stronger dorso-ventral flattening and the distinctly triangular shape of pseudoalveolus. There is little doubt about the specific independence of these two forms. Other representatives of the *Actinocamax mammillatus* species group differ sharply from *A. sternbergi* already in the total lack of granulation. They also differ from it in the same morphological features as *A. depressus* var. *ornata* Moberg.

All other Eurasian *Actinocamas* species, such as *A. primus* Arkhangelsky, *A. plenus* Blainville, *A. strehlensis* Fritsch and Schloenbach emend. Stolley, *A. intermedius* Arkhangelsky s. str. (?=*A. strehlensis* Fritsch and Schloenbach emend. Stolley) and *A. lundgreni* Stolley, completely lack granulation; they also differ from *A. sternbergi* in their much more narrow and rounded double dorso-lateral furrows and in many other morphological features. It is not possible to confuse any of these species with *A. sternbergi* and they shall not be further discussed here.

Locality, Stratigraphic Horizon and Age.—According to Mr. George F. Sternberg (written communication of November 6th, 1957), the only known specimen of *A. sternbergi* (No. 7936-1) was collected from the: "Niobrara Cretaceous chalk, Gove or Logan Co., Kansas. Exact locality not known. Found by George F. Sternberg, exact year not known." Miller (1957, p. 911–12) has accepted the above stratigraphic horizon of this specimen; he has also found it impossible to suggest for it a more precise location within the Niobrara formation.

Some white, chalky matrix was originally present on the alveolar end of the specimen and within the small conical hole on its top; it was scraped off by the writer during the preparation of the specimen. The presence of the chalky matrix agrees with the Niobrara origin of the here discussed specimen; it does not, however, prove it by itself. As mentioned by Mr. Myrl V. Walker (*see* above), similar chalky beds also occur in the Fairport chalky shale of the Carlile formation.

Accepting the Niobrara origin of the here discussed specimen of *A. sternbergi*, its age can range from the latest Turonian to early Campanian (Jeletzky, 1955, p. 882–883). It is to be hoped that additional specimens of this interesting form will be found, which will clarify the position of beds with *A. sternbergi* within the Niobrara formation and their age.

As already mentioned, the only known guard of the closely allied form—*A.* aff. *groenlandicus* Birkelund—was found in the upper Campanian basal conglomerate; it was apparently redeposited from the older Upper Cretaceous rocks and does not, therefore, help to pin down the age of *A. sternbergi*. Another West Greenland form—*A. groenlandicus* Birkelund—belonging to

the same species group with *A. sternbergi*, is more advanced morphologically than the Kansas species. This form was found in beds containing *Inoceramus* aff. *lundbreckensis* McLearn. *Scaphites* of the *S. ventricosus* species group closely allied to *Scaphites saxitonianus* McLearn were, furthermore, found closely above the beds with *A. groenlandicus* (Birkelund, 1956, p. 5–6), which are, therefore, of the early Santonian age Jeletzky, 1960). This suggests that the less advanced *A. sternbergi* is probably of the late Coniacian or earliest Santonian age.

Origin of Name.—This interesting form was named in honour of Mr. George F. Sternberg, Curator of the Museum of Fort Hays Kansas State College, Hays, Kansas, who collected the holotype of the species and kindly lent it to the writer for study.

ACTINOCAMAX WALKERI n. sp.
Pl. 72, Figs. 3A–3D,4A–4C, Text-fig. 3

Diagnosis.—Guard medium-sized, short and fairly stout, weakly lanceolate or subcylindrical in ventral aspect and weakly tapering to almost imperceptibly lanceolate in lateral aspect; apical end long, acute and slightly mucronated; dorso-ventral apical angle varies from 21° to 32°; lateral compression persists throughout the anterior half of the guard, gradually decreasing apicad from the markedly laterally compressed alveolar end; posterior half of the guard is only slightly dorso-ventrally compressed; ventral side of the guard only slightly flattened in the posterior half; surface of the guard virtually smooth, with only a few slight striae here and there; short single lateral furrows, fine, closely spaced double dorso-lateral furrows, and longitudinal, dorso-lateral depressions are all barely perceptible; alveolar end truncated with the surface level or only slightly depressed; a small, rounded, steeply conical hole with the protoconch at the bottom occurs in the middle of truncated alveolar end; 0.5 mm. thick conotheca covers the walls of this hole; surface of conotheca covered by low, small, irregularly shaped tubercles; ventral furrow short (3.5–4.0 mm.), it begins 1.5 to 2.0 mm. above protoconch.

Type Specimen.—The guard reproduced on pl. 72, figs. 3A–3D is herewith selected as holotype of *Actinocamax walkeri* nov. sp.; it is preserved in collections of the Fort Hays State College, Hays, Kansas, Cat. No. 7936-3.

Description.—The following description is based on the study of only two complete guards, one of which is presumed to be full-grown; critical dimensions and ratios of these specimens are given in Table 1.

The adult guard is medium-sized for the genus, short and fairly sturdy. The elongation ratio varies from 6.1 to 7.0; the larger and presumably adult guard being sturdier than the smaller and presumably half grown one.

In ventral (and dorsal) aspect the shape of the guard varies from almost subcylindrical (larger guard) to slightly lanceolate (smaller guard). The maximum lateral diameter is situated either slightly below (in larger guard) or slightly above (in smaller guard) the middle of the guard. From the level of its maximum lateral diameter the larger guard is almost subcylindrical (with only the faintest gradual tapering) all the way orad to the alveolar end in ventral aspect; apicad from the same level the tapering of the guard increases progressively until it reaches the maximum value of 30° to 31° some 15 mm. above the apex; this results in the noticeably convex shape of the apical half of the guard in ventral (and dorsal) aspect; the long and acute apex ends in a slightly separated mucro.

The smaller guard tapers somewhat more clearly and almost evenly all the way orad from the level of maximum diameter to the alveolar end in ventral (dorsal) aspect; apicad from the same level it tapers essentially as the larger guard, except where squashed laterally near the apex.

In lateral aspect the shape of the guard varies from the shape weakly and evenly tapering apicad in larger guard (except for the irregularly collapsed uppermost 8 mm. of the ventral side; *see* below) to the almost imperceptibly lanceolate shape in smaller guard. The maximum dorso-ventral diameter is situated well within the anterior third of the guard; in the larger guard it lies only some 8 mm. below the alveolar end (probably was situated originally at the very alveolar end, the latter having been obviously subsequently deformed; *see* below) and

in the smaller guard it lies only some 18 mm. below the alveolar end. In lateral aspect the larger guard tapers slightly and evenly apicad from the alveolar end (except for the caved in section on the ventral side immed. below the alveolar rim) to the level about 25 mm. above the apical end; further apicad the tapering increases gradually to the base of the mucro, which results in the somewhat convex lateral profile of the guard within this interval; the apical end is long and acute with the dorso-ventral apical angle of 31–32°; it is slightly displaced toward the dorsal side of the guard; in the larger guard the slightly separated, 1.5 mm. long mucro is less apparent in lateral aspect; the smaller guard has about the same lateral outline as the larger one but with the apical dorso-ventral angle of 21–22°; the apical end of this guard is, however, laterally squashed for the distance of about 3 mm. above the tip (pl. 72, figs. 4A,4B), which may have slightly decreased the dorso-ventral apical angle.

The alveolar end of the guard is markedly compressed laterally. The lateral compression persists more than halfway apicad, gradually decreasing in this direction. In the larger guard it only disappears at the level of the maximum lateral diameter where the dorso-ventral diameter (11.7 mm.) becomes about equal to the lateral diameter (11.8 mm.). In the smaller guard the lateral compression disappears some 30 mm. above the apical end where the dorso-ventral diameter (8.3 mm.) about equals the lateral diameter (8.4 mm.). Further apicad both guards are only slightly dorso-ventrally compressed to their apical ends. Only the ventral sides of both guards are slightly flattened throughout their posterior regions; their dorsal sides remain, on the contrary, almost perfectly rounded throughout (Text-fig. 3).

The surface of both guards is almost perfectly smooth. The smaller guard shows only one or two barely perceptible longitudinal, short striae near the alveolar end, and the larger guard, the surface of which is less satisfactorily preserved, shows a few such striae and at least one faint vascular imprint; the latter runs obliquely apicad and toward the dorsal surface of the guard from the more dorsal of the d rble dorso-lateral furrows within the apical third of the guard, forming an angle of less than 30° with that latter.

Faint single lateral furrows are visible under favourable light conditions on both flanks of the smaller guard; they appear about 16 mm. below the alveolar end of the guard close to the ventral side; therefrom these furrows run slightly obliquely for 10–11 mm. orad gradually approaching the middle of the guard's flanks; they end below the squashed alveolar end of the guard. The apparent absence of single lateral furrows on the larger guard is probably due to the strong corrosion of the corresponding parts of its flanks.

The double dorso-lateral furrows are very faint to barely perceptible (pl. 72, fig. 4B) on the upper part of the posterior half of the smaller specimen; they are not visible at all closer to the apex; these furrows run strictly longitudinally and straight, are about 0.4 mm. wide, and are separated from each other by some 0.8 mm. wide, slightly elevated interspaces. The flanks of the larger guard are mostly too strongly corroded to observe its double, dorso-lateral furrows.

The dorso-lateral, longitudinal depressions begin at about the middle of both guards and continue orad to their alveolar ends; they are barely perceptible throughout this interval (pl. 72, figs. 3B,4B). On the smaller specimen the double dorso-lateral furrows distinctly bend toward the dorsal side of the guard at the place of first appearance of the longitudinal depressions. These longitudinal depressions do not seem to exceed 2 mm. in width at the place of their first appearance; they gradually widen further orad, mainly at the expense of the convergence of their dorsal margins in this direction, to some 3.0–3.5 mm. just below the squashed alveolar end of the guard. The dorsal margins are slightly edged; shallow and gently rounded, furrows, about 0.75 mm. wide, run just inside of them; these furrows represent the direct continuations of the more dorsal of the above described double dorso-lateral furrows. Barely perceptible, slightly raised, 1.5 to 2.0 mm. wide longitudinal elevations occur in the middle of the longitudinal depressions; only faint traces of furrows occur between these elevations and the ventral margins of the longitudinal depressions; these latter fur-

rows seem to be the extensions of more ventral of the above discussed double dorso-lateral furrows but it was impossible to observe the connection between both on either of the guard's sides.

Only the left dorso-lateral longitudinal depression is preserved on the larger guard (pl. 72, figs. 3B,3C); it is similar to the above described longitudinal depressions of the smaller guard in every respect.

The so called dorsal field of the guard (pl. 72, fig. 3B) is defined on the anterior three-quarters of the length of both guards; it is distinctly limited over their anterior half where it is bordered by the dorso-lateral longitudinal depressions. From the adapical point of its appearance the dorsal field widens slightly and gradually until it reaches the apical end of the longitudinal depressions; therefrom it narrows gradually and almost evenly all the way to the guard's alveolar end. As the dorsal field becomes narrower orad, it becomes somewhat more elevated. In larger guard the dorsal field becomes progressively higher arched orad and is rounded throughout; in the smaller guard, however, it is somewhat flattened throughout its length.

In the larger guard the alveolar end is very irregularly truncated with several irregularly shaped mounds and depressions interrupting its strongly dorsally slanted (about 40°) surface (pl. 72, figs. 3A–3D). The truncated surface mostly exposes the concentric growth-layers of the guard. Their weathering habit is, however, peculiar as the characteristic alternation of elevated and depressed rings of these growth layers is but imperfectly developed in the guard here discussed; nor is the characteristic pattern of the radial ridges and depressions crossing the rings of exposed growth-layers developed with the usual strength and regularity (pl. 72, fig. 3D).

The cross-section of the alveolar end is somewhat irregularly egg-shaped in the larger guard, its maximum lateral diameter being situated closer to the ventral side of the guard. The alveolar end is markedly compressed laterally, the dorso-ventral diameter exceeding its maximum lateral diameter (pl. 72, fig. 3D).

A small, rounded, steeply conical hole about 2.5 mm. deep and 2 mm. wide occurs in the center of the truncated alveolar end of the larger guard; an ill-defined protoconch still filled out with matrix can be discerned at its bottom, it is about 0.70 mm. wide and apparently rounded in cross-section. The walls of this hollow are covered by a 0.5 mm. thick conotheca, the surface of which is mostly covered by low, irregularly shaped tubercles 0.6–0.7 mm. in diameter; several of these tubercles occur on the left-ventral side of the central hole and are somewhat indistinctly visible on its right side in pl. 72, fig. 3B. The central hole is, thus, certainly not a pseudoalveolus but the remainder of the lowermost part of original alveolus.

A somewhat irregularly shaped, partly gaping and obviously strongly etched out fissure crosses the ventral part of the surface of the alveolar end (pl. 72, fig. 3D); it begins inside of the above discussed central hole some 1.5–2.0 (estimated) mm. above the protoconch; the bottom of this fissure plunges gradually apicad as it approaches the ventral rim of the alveolar end; it appears to be more or less straight and forms an estimated angle of 100°–110° with the orad continuation of the guard's longitudinal axis. The fissure is about 4.0 mm. long on the ventral side of the guard below the alveolar rim and is about 1.5 mm. wide near the lower end; therefrom it widens irregularly orad (pl. 72, fig. 3A). This gaping of the ventral fissure is obviously caused by the subsequent weathering of its walls. A 2.0–2.5 mm. long, weak and shallow furrow occurs just below the gaping fissure on the ventral side of the guard; it weakens fast apicad and then disappears entirely. As with other *Actinocamax* forms (Jeletzky, 1950, p. 7–8; this paper, *see* above), it is not clear whether the gaping ventral fissure represents the secondary deepening and broadening of the original ventral fissure, "splitting surface," or both.

The guard's ventral surface is markedly collapsed and twisted around the ventral fissure and furrow (pl. 72, fig. 3C,3D), which results in the noticeable asymmetry of the cross-section of the alveolar end of the guard. Another marked deformation occurs on the alveolar edge of the left flank of the guard where the normally coloured and smooth surface layer of the same is sharply

bent over the outer part of the surface of the truncated alveolar end and covers the edges of the growth-layers of the guard (pl. 72, fig. 3C,3D) over a space 3×5 mm.^{2}. This interesting deformation could apparently only arise after the burial of the guard when the weight of sediment has squeezed out the plastic substance of the uppermost parts of the inner (uncalcified?) layers of the guard adjoining its harder (calcified?) outer layer and caused the latter to bend over and to come to rest directly upon the edges of the harder (calcified?) lower parts of the same inner layers of the guard. It is easy to see that the above observations give additional support to the old idea of the partly or wholly noncalcified (cartillaginous) nature of smaller or larger portions of the alveolar ends of *Actinocamax* guards (Jeletzky, 1946, p. 98–100; 1948).

It should also be noted that the guard's matter has a somewhat abnormal texture for some distance around the ventral fissure; in this area it is whitish-grey coloured (instead of normal brownish-grey colour) and somewhat spongy in texture; furthermore, the growth-layers of the guard and their calcitic prisms, which are clearly visible elsewhere on the alveolar end's surface, do not persist across the above mentioned area (pl. 72, fig. 3D). Another area of the same texture occurs in the deep, dorsally situated depression of the alveolar end (pl. 72, figs. 3B,3D). This abnormal texture of the guard's matter apparently reflects its original imperfect calcification especially as the marked collapse and twisting of the guard's surface occur in proximity of the area of abnormally textured guard's matter. Also the pronounced exfoliation of the guard's matter around the ventral fissure and in the dorsally situated depression of the alveolar end can be explained by the imperfect calcification of these sections of the guard.

In smaller guard of *A. walkeri* the surface of the truncated alveolar end is essentially level with the outer edges of the same; only the dorsal third of this surface is somewhat slanted (pl. 72, fig. 4B). The original cross-section of the alveolar end was probably similar to that of the above described larger guard; it is, however, squashed in exactly the same direction as its apical end (pl. 72, figs. 4A,4B); both deformations must have resulted from the pressure of sediment upon the imperfectly calcified, more or less plastic parts of the buried guard, as was the case with the deformed alveolar end of the larger guard. The cross-section of the alveolar end of the smaller guard now has the shape of a very elongated ellipse, the longer axis of which runs in dorso-ventral direction; the dorsal side of the ellipse is cracked and angularly shaped (pl. 72, fig. 4C). The ellipsoidally deformed shape of the alveolar end is further complicated by several other longitudinal and transverse cracks and some longitudinal wrinkles (pl. 72, figs. 4A,4B). The surface of the alveolar end exhibits two elevated rings of growth-layers separated by a deep circular hollow from 0.3 to 1.1 mm. wide (pl. 72, fig. 4C); this hollow is locally filled out by the white chalky matrix with remnants of spongy-textured guard's substance such as was described in the larger guard; *see* above); it can be assumed that this circular space was originally much wider and that the plastic, incompletely calcified substance, which filled it out, was subsequently largely squeezed out during the guard's deformation.

A small, fissure-like elongated hollow, 2.5 to 3.0 mm. or more in depth, occurs in the middle of the truncated alveolar end of the smaller guard; it is so strongly laterally deformed that neither the position of the protoconch nor the details of the sculpture of the walls of the hollow could be observed. A very thin fissure crosses the ventral surface of the alveolar end; it begins inside of the above discussed central hole but it is impossible to estimate the distance between the protoconch and the beginning of the fissure, except that it could hardly exceed 2.5 to 3.0 mm. The course of the bottom of the fissure appears to be the same as in the larger guard. The ventral fissure on the ventral side of the guard, which is connected with the one running across the surface of alveolar end, is about 3.5 mm. long; the walls of the fissure remain in contact throughout. This, the perfect preservation of these walls, and the perfectly normal appearance of the guard's substance all around the ventral fissure indicate that the latter has essentially retained its original dimensions and character and is a real ventral fissure rather than a secondarily etched out

"splitting surface" or ventral furrow. No shallow ventral furrow, like the one occurring in larger guard, could be observed in the guard here discussed.

Ontogenetic Development.—The character of ontogenetic development could not be studied in either of the two specimens available. The comparison of the shape and proportions of these two specimens indicates, however, that the half grown guards of *A. walkeri* differ from the adult guards only in their somewhat more slender and slightly more lanceolate outline.

Affinities and Differences.—*Actinocamax manitobensis* (Whiteaves, 1889) s. lato is obviously the closest known North American ally of *Actinocamax walkeri;* it agrees with this latter in such essential taxonomical features as the absence of granulation, appearance of the alveolar end (in *A. m.* var *trehernensis*, var. *spicularis*, & var. *kansanus*), value of Schatsky's index (in *A. m.* var. *spicularis*), weakly mucronated appearance of the apical end, general shape of the guard (especially in *A. m.* var. *lawrencii*), shortness and gaping appearance of ventral fissure, and in presence of tubercles and conotheca in the central hole of the apical end (in *A. m.* var. *lawrencii*). It differs, however, from all known varieties of *A. manitobensis* in:

(1) Considerably shorter and sturdier guard;

(2) Almost total absence of longitudinal striae and extreme weakness of single lateral furrows, double dorso-lateral furrows, and longitudinal depressions;

(3) Predominance of lateral compression throughout the anterior half of the guard;

(4) Extreme weakness of dorso-ventral compression and flattening over the posterior half of the guard;

(5) Peculiar deformations of the apical and alveolar ends of the guard, which are completely unknown in *A. manitobensis*.

The sum total of these distinctions indicates in the writer's opinion, that *A. walkeri* is not conspecific with *A. manitobensis*. The distinctions of both species are well illustrated by the comparison of the figured specimens of *A. walkeri* with representatives of *A. manitobensis* f. typ. and *A. manitobensis* var. *kansanus* described and figured in this paper.

From *Actinocamax sternbergi* our species differs sharply already in the complete absence of granulation and in the quite different character of its double dorso-lateral furrows. Considering these and several other less important morphological differences, these two species can hardly be closely allied, let alone conspecific.

The extremely variable *A. westfalicus* (Schlüter) is, perhaps, the closest ally of *A. walkeri* among the European *Actinocamax* forms. As a rule, *A. weslfalicus* differs clearly from *A. walkeri* in the following features:

(1) Shorter and sturdier guard;

(2) More or less depressed alveolar end;

(3) Somewhat greater dorso-ventral flattening;

(4) More obtuse, shorter and more distinctly mucronated apical end of the guard;

(5) Consistently smaller size;

(6) Moderate to very strong development of single lateral furrows, double dorso-lateral furrows, longitudinal striae, and vascular imprints. Granulation is also often present in more advanced representatives of the species;

(7) Absence of conotheca and tubercles in the pseudoalveolus.

Some extreme representatives of *A. westfalicus*, such as the most primitive representatives of the species figured by Schlüter (1876, pl. 53, figs. 17,18) from Bornholm Island, are indistinguishable from *A. walkeri*, as far as features (1) to (4) are concerned. Even they are, however, markedly sculptured and considerably smaller than the Kansas form in addition to lacking conotheca and tubercles in the central hole of the alveolar end of their guards. There is, therefore, little doubt that *A. westfalicus* is specifically distinct from *A. walkeri*. It is not clear whether the far reaching similarity of some representatives of *A. westfalicus* to *A. walkeri* is in the nature of homoeomorphy or indicates the close affinity of the two species. Considering that the morphologically most primitive representatives of *A. westfalicus* appear to be its oldest forms, which give rise to the more advanced forms of *A. westfalicus* (Stolley, 1897, p. 276–277), it appears possible that *A. westfalicus* is a descendent of *A. walkeri*. More data on the morphology and age of the latter species is needed, however, to clarify its relationships with *A. westfalicus*.

Actinocamax strehlensis Fritsch and Schloenbach s. str. and *A. intermedius* Arkhangelsky s. str. (probably synonymous with the first species) differ from *A. walkeri* in:

(1) More or less depressed character of their alveolar end;

(2) More pronouncedly lanceolate guard;

(3) Shorter and more obtuse apical end of the guard;

(4) More extensive and stronger dorso-ventral compression and flattening of the guard;

(5) Absence of conotheca and tubercles in the pseudoalveolus.

Actinocamax intermedius is, furthermore, rather strongly sculptured. The guard of this species is covered with numerous longitudinal striae; it also has well developed single lateral furrows, double dorso-lateral furrows, dorso-lateral longitudinal depressions, and even a few vascular imprints (Arkhangelsky, 1912, p. 582). All these taxonomically important distinctions make it obvious that the above mentioned Eurasian forms are specifically distinct from *A. walkeri*.

Actinocamax lundgreni Stolley (inclusive of *A. bornholmensis* Stolley) has a deeper pseudoalveolus than either *A. strehlensis* s. str. or *A. intermedius* s. str.; in addition it has a distinctly triangularly shaped alveolar end, fairly to strongly dorso-ventrally compressed and flattened guard, shorter, more obtuse and more distinctly mucronated apical end than *A. walkeri*. The majority of representatives of *A. lundgreni* are, finally, just as strongly sculptured as *A. westfalicus* (except for the granulation). There is, therefore, little doubt that *A. lundgreni* Stolley is specifically distinct from *A. walkeri*.

Locality, Stratigraphic Horizon, and Age.—According to Mr. George F. Sternberg (written communication of November 6, 1957) both specimens of *Actinocamax walkeri* were collected from the: "Niobrara Cretaceous chalk, Gove or Logan Co., Kansas. Exact locality not known. Found by George F. Sternberg, exact year not known."

Some white or orange-tinged, chalky matrix was originally present in the central holes and other depressions of alveolar ends of both specimens; it was removed by the writer during their preparation. The presence of the chalky matrix agrees with the Niobrara origin of *A. walkeri*, although it does not prove it by itself. Mr. Myrl V. Walker (*see* above) mentions, indeed, that similar chalky beds also occur in the Fairport chalky shale of the Carlile formation.

Accepting the Niobrara origin of both specimens of *A. walkeri*, the age of the species can range from the latest Turonian to early Campanian (Jeletzky, 1955, p. 882–883). The close affinity of *A. walkeri* to *A. manitobensis* and *A. westfalicus* and the general evolutionary grade of the former species make it probable that *A. walkeri* was collected in beds of the Coniacian age, that is in the Fort Hays member of the Niobrara formation.

Origin of Name.—This interesting form was named in honour of Mr. Myrl V. Walker of Fort Hays State College, Hays, Kansas.

ACTINOCAMAX sp. aff. A. LAEVIGATUS
Arkhangelsky, 1912
Text-figs. 4a–4d,5a–5d

Material.—Two small, fragmentary guards of the collection cannot be compared with any of the hitherto described North American *Actinocamax* forms but are morphologically similar to the little known *Actinocamax laevigatus* Arkh. from the Lower Campanian (zone of *Pteria tenuicostata*) of the European Russia. These Kansas guards are probably not conspecific with the Russian species and new; they are, however, inadequate as the basis of a new species and could, furthermore, be but juvenile representatives of one of the previously described North American *Actinocamax* species and varieties.

Description.—Guard small, long, and slender; the assumed length of smaller specimen #10368 is around 42 mm., of which only the anterior 32 mm. are preserved; the assumed length of the larger specimen #8126 is about 53 mm., of which only the anterior 38 mm. are preserved.

In ventral and dorsal aspects the shape of the guard varies from almost subcylindrical (text-fig. 4b) to weakly lanceolate (text-figs. 5a,5c); in lateral aspect it varies from regularly subcylindrical (text-figs. 4a,4c) to slightly lanceolate (text-fig. 5b).

The maximum lateral diameter is situated within the estimated posterior half in both guards. From the level of their maximum lateral swelling both guards taper gradually and evenly all the way to the base of their

protruding alveolar ends; the tapering is, however, more pronounced in the guard #8126, which results in its much more narrow cross-section at the base of the protruding alveolar end (text-figs. 5a,5c). In ventral and dorsal aspects both guards taper slightly apicad from the level of their maximum swelling to their broken off apical ends; their shape below the posterior breaks is unknown. A reconstruction of the missing apical parts of both guards is, however, attempted in text-figs. 4,5.

In lateral aspect the maximum diameter is situated within the posterior part of the guard in the specimen #8126; from this level this guard tapers gently and evenly, but less noticeably than in the ventral aspect, all the way to the base of its protruding alveolar end (text-fig. 5b). Apicad, the guard #8126 tapers evenly but almost imperceptibly all the way from the level of its maximum swelling to the broken off apical end. The guard #10368, on the contrary, has its maximum dorso-ventral diameter of 3.9 mm. only 10 mm. below the alveolar end; further apicad it tapers slightly but more or less evenly to the level some 9.0 mm. above the broken off apical end. Therefrom to the posterior fracture the tapering increases slightly and gradually, which results in the slightly convex outline of the guard throughout this interval.

Strong lateral compression persists throughout the estimated anterior half of both guards; it is accompanied by the distinct flattening of their lateral sides throughout most of this interval. In the larger specimen #8126 the lateral diameter at the base of its protruding high conical alveolar end is only 2.7 mm. as compared with the dorso-ventral diameter of 3.7 mm.; in the smaller specimen #10368 the corresponding diameters are 3.3 and 3.9 mm. The cross-section of both guards at that level is, therefore, egg-shaped; its dorsal side representing the pointed end of the egg and the ventral side its obtuse end.

The lateral compression gradually decreases apicad until both diameters become virtually equal about midway apicad in both guards. In larger specimen #8126 the lateral flattening disappears some 29 mm. below its alveolar end, at about the level of its maximum swelling; there both diameters are 5.1 mm. and the guard's cross-section is almost perfectly circular; in the smaller specimen #10368 the lateral flattening disappears about 22 mm. below its alveolar end where both diameters are 3.9 mm. and the cross-section is again almost perfectly circular. Further apicad the cross-section remains almost perfectly circular and the diameters almost to quite equal in both guards; the cross-sections of their broken off apical ends are shown in text-figs. 4d and 5d. There they show slight dorso-ventral compression (ratio lateral/dorso-ventral diameters is 5.8..5.7 mm. in the larger guard and 3.2..3.1 mm. in the smaller guard) and some flattening of the ventral side in both guards. Both features can, however, be due to the corrosion of the surface of the guards, which is present in both instances.

The surface of both investigated guards is perfectly smooth, except for two or three short and weak longitudinal striae on the ventral surface of the smaller guard (#10368) closely below its protruding, cone-shaped alveolar end (text-fig. 4b). The striation could have been more extensive originally, however, as both guards appear to be somewhat corroded over considerable parts of their surface.

No traces of single lateral and double dorso-lateral furrows are perceptible on either of the guards.

Dorso-lateral, single, longitudinal depressions occur over the anterior regions of both guards (text-figs. 4a,4c,5a); they are barely perceptible in favourable light, except closely below the base of the protruding alveolar end where their dorsal margins are somewhat better defined and may be slightly incised. The ventral margins of the depressions are barely perceptible even in favourable light throughout and appear to be strictly longitudinal. No sculpture of any kind is discernible within the depressions, which are only 0.5–0.6 mm. wide at the apical end but widen to some 1.0 to 1.5 mm. just below the cone-shaped, protruding alveolar end.

The dorsal margins of the longitudinal depressions gradually converge orad (text-figs. 4a,4c,5a). This results in the gradual but marked narrowing of the dorsal field of the guard toward its alveolar end accompanied by the equally gradual but slight increase of its protrusion (text-fig. 5a). Be-

cause of this convergence, accompanied by the marked compression and flattening of the lateral sides of the guard throughout its alveolar region, the dorsal field of the guard becomes quite narrow and prominent in the proximity of its alveolar end. In the larger guard #8126 it is somewhat keel-shaped over the 8–9 mm. long interval adjoining its alveolar end; the same phenomenon is less apparent in the smaller guard #10368, where the dorsal field remains flat-topped throughout the alveolar region.

The alveolar end of the guard strongly protrudes and forms a more or less regularly shaped cone. The shape and appearance of the alveolar end differs, however, somewhat in the two guards studied. In the smaller guard #10368 the cone is regularly shaped but somewhat asymmetrical in lateral aspect, its top being somewhat displaced toward the dorsal side of the guard (text-figs. 4a–4c). The cone is distinctly separated from the subparallel sides of the guard in both ventral and lateral aspects. The hitherto subparallel sides of the guard start to converge orad at about 35° in the lateral aspect at the base of the cone and maintain this angle to its top. In ventral and dorsal aspect the angle of the cone is only 22°–23°. The boundary between the postalveolar part of the guard and its protruding alveolar cone rises somewhat toward the dorsal side of the guard. The height of the protruding cone decreases accordingly from 5.5 mm. on its ventral side to some 4.5 mm. on its dorsal side (text-figs. 4a, 4c).

The surface of the protruding cone is almost smooth in the guard #10368; the edges of the guard's growth-layers exposed in it are mostly only visible as faint concentric striae without any relief. Only in two or three instances do they form faint concentric ridges, shown in somewhat accentuated form on text-figures 4a and 4c. No radial ridges and depressions are present on the protruding alveolar end of the specimen #10368. These features are in contrast with the normal appearance of the protruding alveolar end of the guard in *Actinocamax*.

The protruding alveolar end of the guard #8126 is much less regularly conical in its shape than that of the guard #10368; it is, however, almost symmetrical in lateral aspect (text-fig. 5b). In the guard #8126 the boundary between the postalveolar part of the guard and its protruding alveolar cone is rather irregular and much less distinct than in the guard #10368. The gradual and even orad tapering of the postalveolar part of the guard only increases somewhat at this boundary. This increase is slight in dorsal and ventral aspects (text-figs. 5a,5c); it is, however, fairly pronounced in lateral aspect (text-fig. 5b) where the angle of the cone reaches 25°–27°.

On the right side of the guard (see text-fig. 5c) the alveolar cone is only about 2 mm. high, the whitish-discoloured surface layer of the guard continuing unbroken to that level. On the left side of the guard, however, the cone is interrupted by several irregularly concentrical, narrow ridges of the growth-layers of the guard; narrow depressed grooves of the same irregularly concentrical pattern separate the above ridges from each other. On ventral and dorsal sides of the guard the above narrow ridges and grooves rise steeply but irregularly; most of them disappear, however, beneath the preserved tongue of the surface layer of the guard close to its previously described right side.

A steeply and somewhat irregularly conical hole, only 1 to 1.2 mm. wide and less than 1 mm. deep occurs near the top of the protruding alveolar cone; it probably represents the partly corroded protoconch. This hole is situated centrally in both guards studied; its position does not coincide, however, with the tops of their alveolar cones. In the guard #10368 the hole is displaced ventrally and slightly to the left of the top of the avleolar cone (text-figs. 4b,4c). In the guard #8126, however, it is on the left side of the alveolar cone (text-fig. 5b). No traces of the ventral fissures or ventral furrows were observed on either of the two guards studied.

Ontogenetic Development.—The character of the ontogenetic development could not be studied in any of the two specimens available. Assuming that the smaller guard is the half grown representative of the same species as the larger guard (#8126), the guard's outline changes noticeably in the course of its ontogeny from virtually subcylindrical to weakly lanceolate in lateral and ventral aspects. The guard also acquires a more narrow cross-section at the alveolar end, as it grows.

Localities, Stratigraphic Horizon, and Age.—The smaller specimen is known to be from the lower part of the Niobrara formation. Mr. Myrl V. Walker comments on it as follows (letter of January 24th, 1958) "Specimen #10368 was collected by one of my students this past fall when we were on a class field trip. I would estimate that it came from the Smoky Hill chalk not more than fifty (50) feet above the Fort Hays limestone."

The larger specimen #8126 was collected from the: "Niobrara Cretaceous chalk, Gove or Logan Co., Kansas. Exact locality not known. Picked up by George F. Sternberg, exact year not known." It seems probable, however, that it comes from about the same level within the Niobrara formation as the specimen #10368.

The occurrence of *Uintacrinus* near the base of the Smoky Hill chalk in the eastern Gove County and elsewhere (Miller, Jr., Sternberg, & Walker, 1957, p. 166) suggests that *Actinocamax* sp. aff. *A. laevigatus* occurs in rocks of the late Santonian age. This conclusion is supported by the fact that one of its European allies—*Actinocamax laevigatus* Arkh.—was found in the rocks of the Lower Campanian age (*see* above), while the other —*Actinocamax quasiverus* Naidin, 1953—was found in the Santonian (probably Upper Santonian) rocks of the Crimea.

Other allied *Actinocamax* of the species group of *A. verus* Miller, 1826 are also largely restricted to the Santonian and Lower Campanian rocks. This, too, agrees well with the above suggestion of the occurrence of *Actinocamax* sp. aff. *A. laevigatus* Arkhangelsky in the upper Santonian rocks of Kansas.

Affinities and Differences.—*Actinocamax* sp. aff. *A. laevigatus* Arkh. is a representative of the specialized species group of *Actinocamax verus* Miller. This species group is characterized by the small size of the guard combined with the presence of the high, conically shaped alveolar end of the same. Although characteristic of the majority of its representatives, neither the absence of single lateral furrows and of the ventral furrow (or fissure) nor the presence of the peculiar, transversely corrugated, fine granulation of the surface of the guard is characteristic of all representatives of this group. Nor are these features restricted to this group alone.

From its closest ally—*Actinocamax laevigatus* Arkhangelsky—our form differs in:

(1) Much lower and asymmetrically protruding alveolar end of the guard;

(2) Much longer and more slender guard;

(3) Absence of the ventro-alveolar furrow; and

(4) Less regularly conical shape of the protruding alveolar end.

In spite of the apparently complete likeness in all other respects, the above mentioned distinctions appear to be ample for the assumption of the specific independence of these two forms.

From somewhat less similar *Actinocamax quasiverus* Naidin, 1953 our form differs in:

(1) Much longer and more slender guard;

(2) Absence of numerous, fine, longitudinal striae and very fine granulation (near alveolar end) characteristic of *A. quasiverus*.

(3) Somewhat less protruding alveolar end of the guard.

From *Actinocamax verus* Miller, 1826 and its varieties our species differs in the same features as from *A. laevigatus* and *A. quasiverus*. All representatives of *A. verus* and its varieties are, besides, more or less distinctly granulated.

Actinocamax sp. aff. *A. laevigatus* Arkh. cannot be confused with any other known *Actinocamax* species.

ACTINOCAMAX sp. indet. A. (? aff. A. MANITOBENSIS Whiteaves, 1889)
Text-figs. 6a–6c

Description.—One, small, elongated and slender guard—No. 7936-4—is too imperfectly preserved to be either referred to any of the here described *Actinocamax* forms or even be compared with any of them, especially as the information available about its stratigraphical position and age is rather scanty.

The guard is about 60 mm. long with a few millimeters of its apical end missing; it is elongated and slender, duplicating in this respect the corresponding ontogenetic stages of the adult guard of *Actinocamax manitobensis* (Whiteaves, 1889) reproduced by Jeletzky (1950, p. 8, text-fig. 1). It is, however, much more slender than the similarly long, juvenile guard of the same species

reproduced by Jeletzky (1950, pl. 1, fig. 1a,1b).

The guard is only slightly lanceolate in lateral aspect and weakly lanceolate in ventral aspect; its maximum dorso-ventral diameter of about 5.4 mm. is situated about 23 mm. above its broken off apical end; the maximum lateral diameter of 5.9 mm. is situated at about the same level; the surface of the guard is, however, so strongly corroded in its upper two-thirds that the original values and positions of both maximum diameters could easily have been different from the above cited.

The apical end is very acute, the dorso-ventral apical angle being about 16°; its broken off tip is 3.5 mm. in its largest diameter. The tip is, however, strongly deformed in dorso-ventral diameter so as to indicate that it was still capable of plastic deformation under the pressure of sediments after the burial of the guard. These deformations were already discussed in detail on connection with the discussion of other Kansas *Actinocamax*.

The guard is markedly compressed dorso-ventrally in its best preserved posterior third (d/v. diam. 5.2 mm. vs lat. diam. 5.8 mm. at the level of 14 mm. above the apex) and its ventral and dorsal sides are markedly flattened throughout this interval. The upper two-thirds of the guard are so strongly corroded as to make its original cross-section unrecognizable.

All traces of original sculpture of the surface, as well as those of single lateral and double dorso-lateral furrows and of the longitudinal depressions, are obliterated by the above mentioned corrosion.

The alveolar end of the guard is squashed in the same fashion as is its apical end and generally speaking in the same direction; the cause is believed to be the same in both instances. A 3.3 mm. long and 0.7 mm. wide, shallow ventral furrow occurs below the jagged outer rim of the alveolar end. The surface of the alveolar end is slightly but quite irregularly depressed forming a pseudoalveolus some 1.0 to 1.5 mm. deep; the protoconch is not preserved and it is probable that the pseudoalveolus reaches below its level. The concentric growth-layers of the guard and the transverse ridges are only very poorly developed. The deformation of pseudoalveolus is accompanied by the formation of 1–3 mm. long longitudinal furrows and transverse tension cracks at its outer edges and for some 8 mm. apicad therefrom.

Remarks.—The guard discussed above is very similar to the more slender types among the juvenile guards of *A. manitobensis* (Whiteaves, 1889). This guard could, therefore be a juvenile guard of *A. manitobensis;* it is, however, also indistinguishable from the guards of *A. primus* var. *elongata* Arkh. This guard could, furthermore, equally well be a juvenile guard of some other *Actinocamax* species, especially because it was probably collected in the Niobrara formation and so probably is of the latest Turonian to early Campanian age. The specimen here discussed was, therefore, left specifically unassigned.

Locality, Stratigraphic Position, and Age.—According to its museum label, the specimen here discussed was collected: "from the Niobrara Cretaceous chalk, Gove or Logan County, Kansas; exact locality not known. Found by George F. Sternberg, exact year not known." Some white to yellowish-grey chalky matrix still adheres to the excavated fracture of its apical end and to its depressed pseudoalveolus, which agrees with the Niobrara origin of the *Actinocamax* sp. indet. A. here discussed. As mentioned by Mr. Myrl V. Walker, however (p. 513), similar chalky beds also occur in the Fairport chalky shale of the Carlile formation.

Accepting the Niobrara origin of the *Actinocamax* sp. indet. A, here discussed, its age could range from the latest Turonian to the early Campanian.

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A NEW NAUTILOID, *EUTREPHOCERAS EYERDAMI*, NEW SPECIES FROM THE COWLITZ FORMATION, UPPER EOCENE, OF WASHINGTON

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ABSTRACT—*Eutrephoceras eyerdami* Palmer, n. sp., is described from the Cowlitz formation, upper Eocene of Washington. Although fragments of *Eutrephoceras* have been reported from the locality the present shell is the first to be preserved well enough for specific naming. The specimen was found by Walter J. Eyerdam at the type locality of the Cowlitz formation, on the Cowlitz River, near Vader, Lewis County, Washington.

INTRODUCTION

IN NOVEMBER, 1959, Walter Eyerdam of Seattle, Washington, sent me a nautiloid specimen from the bank of the Cowlitz River, near Vader, Lewis County, Washington, Cowlitz formation, upper Eocene. The fossil proved to be an *Eutrephoceras*. Although the find consists of a single incomplete conch, it is well preserved. It was broken naturally so that the inner nature of several camerae, including the septa and two septal necks, were exposed. Because of the rarity of *Eutrephoceras* in the Tertiary on the West Coast, particularly Washington, the species is herein described. Search in the West Coast nautiloid literature revealed that Arnold and Hannibal (1913) found a specimen in the Cowlitz formation on the Cowlitz River and listed the form as *Aturia mathewsoni* Gabb. The fossil (S.U. 523) was illustrated by Schenck (1931). It was again figured by Miller (1947) and determined by him as *Eutrephoceras*. A second fragment (S.U. 7900) from the Stanford University collections was also included in *Eutrephoceras* and illustrated by Miller (1947). One cannot state that those fragments belong to the same species as Eyerdam's shell.

Eutrephoceras eyerdami was found in the bluff at the bend of the Cowlitz River about 1½ miles east of Vader (old Little Falls, Sopenah), Lewis County, Washington, which is the type locality of the Cowlitz formation (Weaver, 1912) of upper Eocene age. This is equivalent to localities 232, 233, and 327, Wash. Geol. Sur. (Weaver, 1916a, 1916b, 1916c, 1937, 1942; Weaver and Palmer, 1922). The Cowlitz formation consists of a series of marine, brackish, and fresh-water sediments intercalated with volcanic rocks in the area of the Cowlitz River where the Olequah-Stillwater Creeks enter the Cowlitz near Vader. The formation extends north to south of Winlock, Lewis County. It is now believed to be more than 8000 feet thick (Hendricksen, 1956). The portion at the Cowlitz bluff represents about 200 feet (Weaver, 1937) of the formation.

Although the fossils along the Olequah (Olequa) and Stillwater Creeks are abundant, well preserved, and include brackish, fresh-water, and marine forms, those at the type bluff on the Cowlitz represent a marine phase. There, a typical upper Eocene molluscan fauna has been known since Arnold and Hannibal's (1913) early collecting. The locality has been the source of extensive collecting by geologists from Washington, California, and Oregon. The preservation of the fossils is as perfect as those of the Eocene of the Paris Basin or from the Gosport sand of the middle Eocene at the famous Claiborne Bluff, Alabama. A complete bibliography of the literature on the locality, the Cowlitz formation, or the fossils is not appropriate in this article. Suffice it to say that the works of Charles E. Weaver (1912, 1916a,b,c, 1937, 1942) include the important geological papers on the area, as author of the formational name and as chief describer of the geology and fauna and illustrator of the fossils. Of the 146 species of mollusks listed by Weaver (1942) from the Cowlitz formation no cephalopods were included. Miller (1947) accounted for the two fragments of *Eutrephoceras* mentioned

herein from the Cowlitz. Those specimens were the individuals which Arnold and Hannibal (1913), Weaver (1916c), and Schenck (1931) listed as *Aturia mathewsoni* or *Nautilus* sp. The writer made extensive collections for the Washington State Geological Survey in 1917 from the Cowlitz formation at the Cowlitz section of the type locality as well as on Olequah Creek and Stillwater Creek in the vicinity of Vader. Large collections had been made earlier by the Washington Geological Survey parties. Therefore, the report of only three specimens from the Cowlitz locality indicates the sporadic and fortuitous occurrence of the nautiloid.

Systematic Description

Family Nautilidae d'Orbigny, 1840

Genus Eutrephoceras Hyatt, 1894

Type species.—By original designation, *Nautilus dekayi* Morton (1834, pl. VIII, fig. 4). [Navesink marl, Upper Cretaceous, New Jersey.] "Loc., Dakotah, Cretaceous"—Hyatt.

Range of genus.—Upper Jurassic—Miocene. World-wide.

As has been pointed out by authors (Reeside, 1924; 1927; Miller & Thompson, 1933; Miller, 1947), although Hyatt gave a specific type species designation with reference to the New Jersey Cretaceous shell he mixed his description with the statement of locality, description, and figures of specimens of the form from the Cretaceous of "Dakotah" (Meek, 1876) (Montana and South Dakota). That species Hyatt identified as *E. dekayi* (Morton) but it is now regarded as a distinct species (*E. montanaensis* Meek). Although the type species designation is confused, the generic definition is not disrupted.

Eutrephoceras eyerdami Palmer, n. sp.

Pl. 73, figs. 1–6

Conch incomplete, subglobular in shape, surface smooth; a small portion of the outer lateral area of test preserved revealing growth lines with a slight sinus adapertural; faint longitudinal striations are visible, sharper on the ventral margin. These are similar to those observed on the shell of living *Nautilus*; umbilicus fairly deep, outermost margin about 10 mm. across, filled with rock matrix; septa of phragmocone preserved in part and two septal necks intact (see figs. 1,2,5); siphuncle situated slightly dorsad (fig. 2); sutures nearly straight, curving dorsad.

Measurements: Greatest diameter, 75 mm.; greatest width of phragmocone, 48± mm.; width of umbilicus, about 10 mm.; length of preserved septal neck, 5+ mm., angle of inclination of septal neck about 30°.

Eutrephoceras spp. in Miller (1947, p. 38, pl. 16, figs. 7,8; pl. 48, fig. 4) differ from *E. eyerdami* in the greater breadth, although such a difference might be accounted for by sex. The siphuncle in the fragment (pl. 48, fig. 4) is more dorsad than on the present specimen. Miller considered that the two fragments were probably conspecific. They could well be. The genus is represented in the Eocene on the Pacific Coast of the United States: in California, by *E. ?hallidayi* (Waring) and *E. stephensoni* (Dickerson) from the Paleocene (Martinez), *E. hannai* Vokes from the La Jolla formation, middle Eocene, and *E. marksi* Miller, Tejon formation, upper Eocene; in Oregon there are fragments from the upper Eocene or lower Oligocene and *E. oregonense* Miller from the Oligocene; in Washington, fragments and *E. eyerdami* from the Cowlitz formation, upper Eocene. Of these species *E. eyerdami* bears the closest resemblance to *E. marksi* Miller from the Tejon of California. The holotype of that species is a larger shell than the present form. *E. eyerdami* is not so broad as *E. hannai* and has a wider umbilicus. Unfortunately the species are known by so few specimens that age and sexual variations cannot be determined.

Occurrence.—At bend in Cowlitz River, 1½ miles east of Vader, Lewis County, Washington. Cowlitz formation, upper Eocene. Collected by Walter J. Eyerdam, 1956.

Holotype.—No. 6066, Paleontological Research Institution.

It is a pleasure to name this species for its discoverer, Walter J. Eyerdam, of Seattle, Washington.

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Page and plate references include only the pages and plates pertinent to this article and not the complete pagination of the publication excep-

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MANUSCRIPT RECEIVED MARCH 20, 1960

EXPLANATION OF PLATE 73

FIGS. *1–6*—*Eutrephoceras eyerdami*, n. sp. Holotype, P.R.I. 6066. *1*, natural break showing camerae, septa, and septal neck; *2*, same view to show siphuncle; *3*, exterior view coated with ammonium chloride to show growth lines; *4*, same view uncoated; *5*, septal neck; *6*, ventral view. Measurements, see text.

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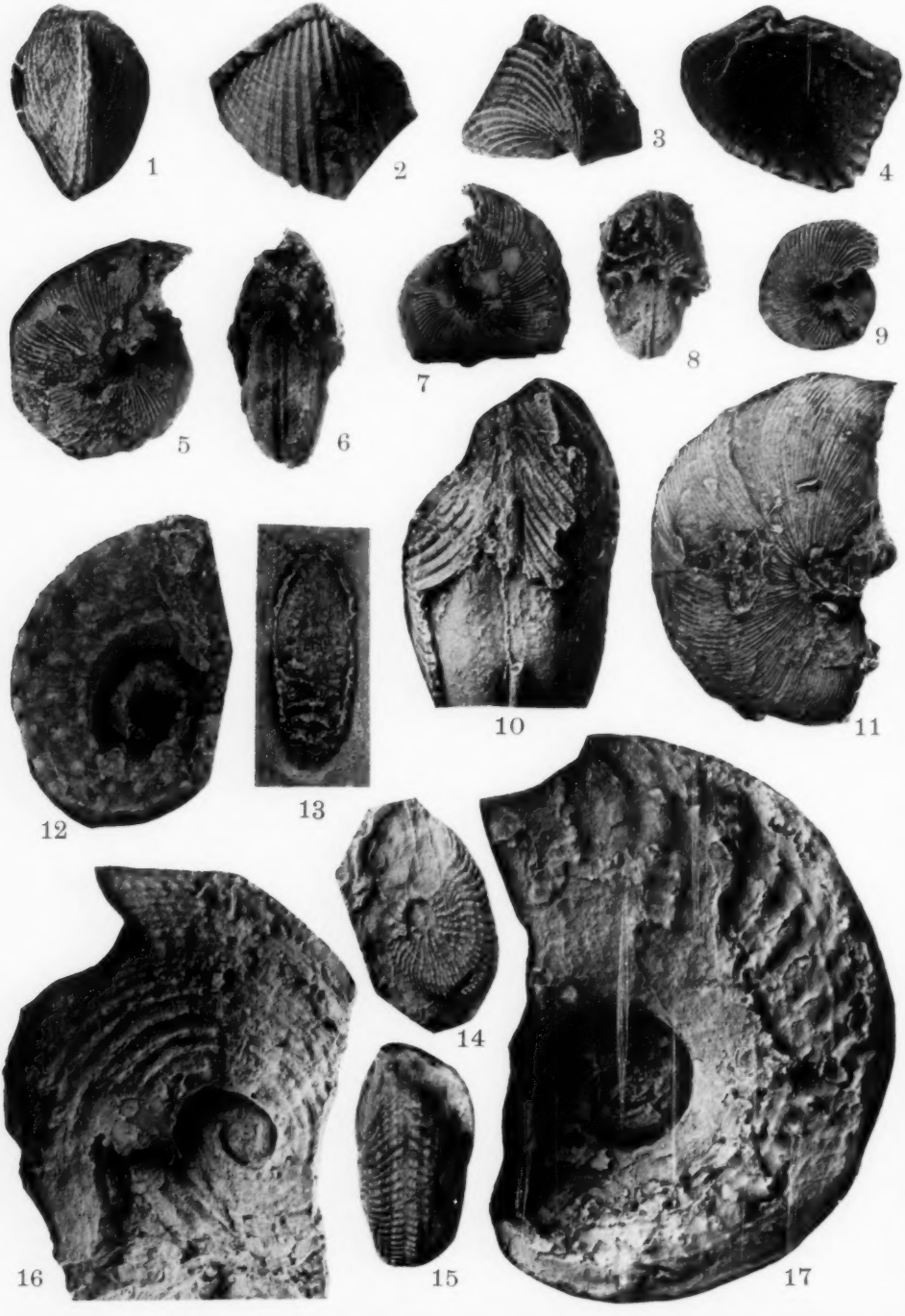
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JOURNAL OF PALEONTOLOGY, V. 35, NO. 3, P. 535–542, PL. 74, 2 TEXT-FIGS., MAY, 1961

UPPER TRIASSIC MARINE MOLLUSKS FROM THE NATCHEZ PASS FORMATION IN NORTHWESTERN NEVADA[1]

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ABSTRACT—Diagnostic ammonites and other fossils indicate that much of the Natchez Pass formation in northwestern Nevada is of early Late Triassic (Karnian) age instead of Middle Triassic age as originally dated. *Trachyceras*, sensu stricto, of early Karnian age occurs in the lower part of the Natchez Pass formation in the East Range and is tentatively identified from a corresponding stratigraphic position in the Humboldt Range. The upper part of the formation in the northeastern foothills of the Humboldt Range has yielded a large upper Karnian fauna including *Paratropites* cf. *P. sulcatus* (Calcara), *Spirogmoceras shastense* (Smith), *Pleuronautilus? alaskensis* Kummel, and *Septocardia?* sp., which are described in this paper.

INTRODUCTION

THE Natchez Pass formation is dominantly a massive marine carbonate rock, is commonly somewhat deformed and sheared and identifiable fossils are scarce. Muller, Ferguson, and Roberts (1951; Ferguson, Muller, and Roberts, 1951) orignally assigned the Natchez Pass formation to the upper Middle Triassic because it overlies the Prida formation containing a rich Anisian (lower Middle Triassic) ammonite fauna, and it underlies the Grass Valley formation which contains Upper Triassic brachiopod and pelecypod faunas. During more recent field study in the type area and in the Humboldt Range to the west, diagnostic fossils have been found at several localities in the Natchez Pass formation and indicate that much of the formation is of early Late Triassic age.

[1] Publication authorized by the Director, U. S. Geological Survey.

OCCURRENCE AND AGE OF FAUNAS

Two ammonites referable to *Trachyceras* (*Trachyceras*) were collected from the Natchez Pass formation at USGS loc. M777 (see locality list at end of paper) about three miles north of the type locality of the formation on the east flank of the East Range (text-fig. 1). Both specimens were found in faintly laminated dolomitic limestone about 400 feet above the base of the formation and about 100 feet stratigraphically below a

EXPLANATION OF PLATE 74

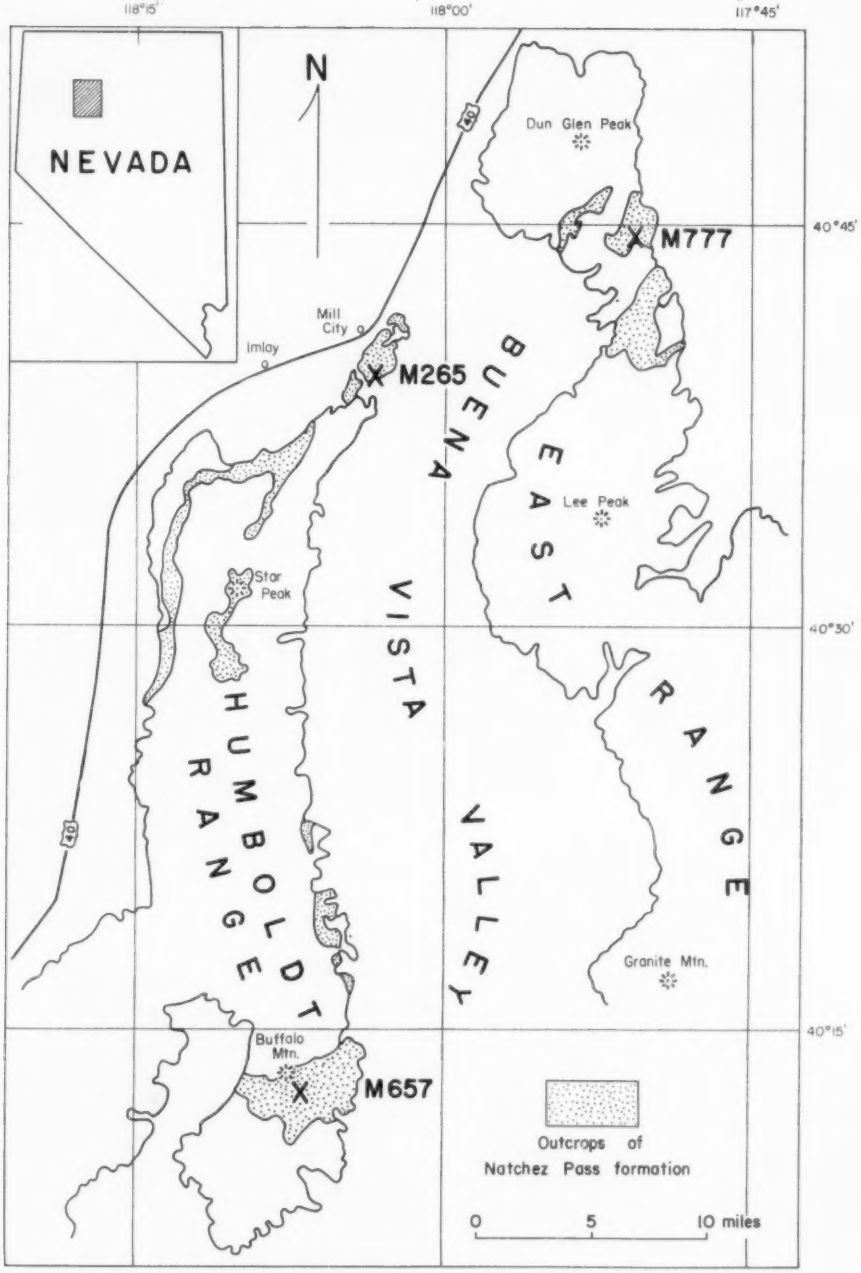
FIGS. *1–4*—*Septocardia?* sp. All figures of latex casts, ×2. *1*, anterior view of incomplete specimen, USNM 130863; *2*, incomplete left valve, USNM 130864; *3*, dorsal view of left valve, USNM 130865; *4*, interior of right valve, USNM 130866.

5–11—*Paratropites* cf. *P. sulcatus* (Calcara, 1845, of Gemmellaro, 1904). All figures of latex casts. *5,6*, lateral and ventral views, USNM 130858, ×1; *7,8*, lateral and ventral views, USNM 130859, ×1; *9*, lateral view, USNM 130860, ×1; *10*, ventral view showing details of keel and ribbing, USNM 130861, ×2; *11*, lateral view, USNM 130862, ×1.

12—*Pleuronautilus?* cf. *P. alaskensis* Kummel, 1953. Lateral view of latex cast, USNM 130857, ×1.

13–15—*Trachyceras* (*Trachyceras*) sp. *13*, ventral view of a weathered incomplete specimen, USNM 130853, ×1; *14,15*, lateral and ventral views of a secondarily deformed specimen, USNM 130854, ×1.

16,17—*Spirogmoceras shastense* (Smith). Both figures of latex casts, ×1. *16*, lateral view of specimen with strigate ornamentation, USNM 130855; *17*, lateral view of specimen showing transition from strigate to coarse radial ornamentation, USNM 130856.

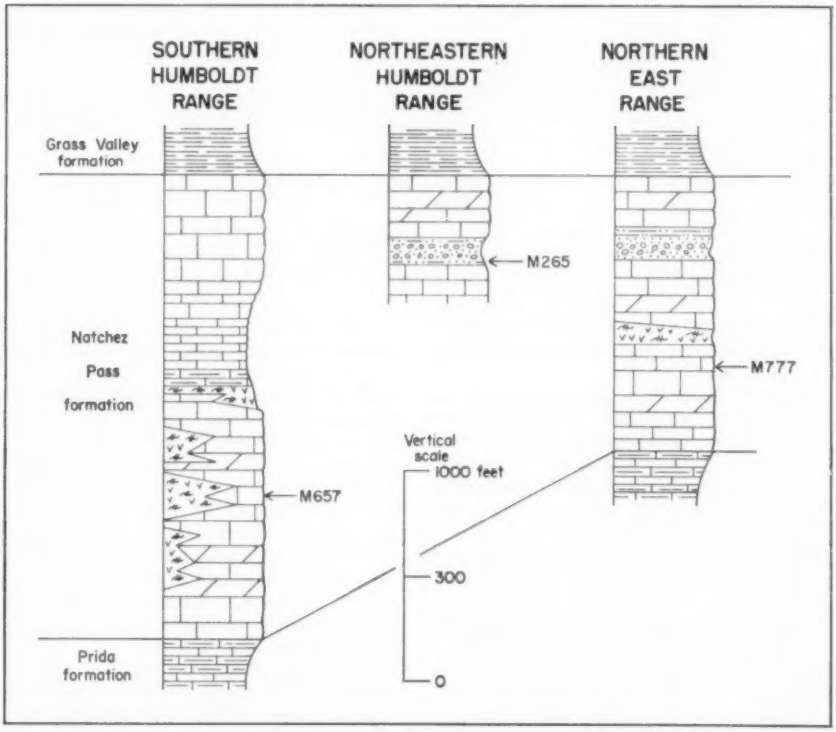


TEXT-FIG. 1—Index map showing the location of fossil collections made from the Natchez Pass formation in the East and Humboldt Ranges, Nevada.

basic volcanic breccia which is part of a volcanic unit that characterizes the middle part of the formation in this area (text-fig. 2).

Trachyceras, sensu stricto, is generally regarded as an index of the lower Karnian (lowest Upper Triassic). The two specimens described herein are secondarily deformed, but are closely similar to *Trachyceras* (*Trachyceras*) *desatoyense* Johnston which occurs with an ammonite fauna characteristic of the lower Karnian *Trachyceras aon* or *T. aonoides* zone in the New Pass Range, Nevada (Johnston, 1941).

Trachyceratid ammonites have also been found at a number of places in the lower part of the Natchez Pass formation in the Humboldt Range. Most of these fossils, however, are too poorly preserved for positive subgeneric assignment to *Protrachyceras* or *Trachyceras*, or for use in discrimination of the Middle Triassic-Upper Triassic boundary. A single specimen, questionably referred to the subgenus *Trachyceras*, was collected in association with abundant bone fragments from a thin limestone tongue between volcanic rocks at USGS loc. M657 on the southeast slope of Buffalo Mountain at the south end of the Humboldt Range. Here, basic volcanic flows and breccias intertongue with the carbonate rocks of the lower part of the Natchez Pass and make up a much greater share of the section than they do farther north and east. Nevertheless, this locality roughly corresponds in stratigraphic position within the formation to that from



TEXT-FIG. 2—Generalized columnar sections showing the stratigraphic position of fossil collections made from the Natchez Pass formation in the East and Humboldt Ranges, Nevada.

which the specimens of *Trachyceras* were obtained in the East Range.

The largest fauna thus far obtained from the Natchez Pass formation is from USGS loc. M265 in the upper part of the formation south of Mill City in the low hills that form the northeasternmost appendage of the Humboldt Range. These fossils occur as well-preserved molds in calcareous siltstone at the base of a siltstone, sandstone, and chert-pebble conglomerate unit in the inverted limb of a large syncline, overturned to the northwest. This clastic unit is thought to be equivalent to that in the East Range section near the top of the Natchez Pass formation and several hundred feet above the occurrence of *Trachyceras* (fig. 2). The fauna from M265 comprises cephalopods, pelecypods, and brachiopods, among which the following forms have been recognized:

**Paratropites* cf. *P. sulcatus* (Calcara, 1845, of Gemmellaro, 1904)
**Spirogmoceras shastense* (Smith, 1904)
Clydonitid? ammonite; one immature specimen
**Pleuronautilus?* cf. *P. alaskensis* Kummel, 1953
Proclydonautilus sp.
**Septocardia?* sp.
Alectryonia sp.
Placunopsis sp.
Gervilleia sp.
Cassianella sp.
Pinna sp.
Palaeoneilo sp.
Pectinid pelecypod
Spiriferoid brachiopods

The four species marked with an asterisk are the most useful for dating this assemblage and are described below.

Paratropites cf. *P. sulcatus* is perhaps the most abundant element in the fauna from M265. The genus *Paratropites* is representative of the *Tropites subbullatus* zone of late Karnian age, though some species are known from older Karnian zones in the Alps (Mojsisovics, 1893, p. 796). The species with which the Natchez Pass forms are compared is from the undifferentiated Upper Triassic of Sicily, and, unfortunately, neither it nor the associated forms have been recognized in the Alpine succession of zones. *Spirogmoceras shastense* is known from the so-called Hosselkus limestone in Shasta County, California, where it is associated with many species in common with, or closely related to, those of the *Tropites subbullatus* zone (Smith, 1927). The nautiloids probably cannot be relied upon as having narrowly restricted stratigraphic ranges; however, *Pleuronautilus alaskensis* was described from the Chitistone limestone of Alaska (Kummel, 1953, p. 36–37), from which a late Karnian fauna is known (Moffit, 1938, table facing p. 52). A number of fragmentary carditoid pelecypods assigned to *Septocardia?* are present, but the brachiopods and the various other pelecypods are represented by only one or two individuals. Although the application of the name *Septocardia* Hall and Whitfield is in doubt, pelecypods provisionally assigned to this genus are known from several localities in the Upper Triassic of Nevada. Those most closely resembling the forms from the Natchez Pass formation are from the Pilot Mountains at the base of the upper limestone member of the Luning formation, considered middle or late Karnian in age by Muller and Ferguson (1939, p. 1598). The pelecypods and brachiopods may not be indicative of a precise age, but they do not conflict with the late Karnian age assigned this fauna on the basis of the cephalopods.

SYSTEMATIC DESCRIPTIONS

Order AMMONOIDEA

Genus TRACHYCERAS Laube, 1869

Subgenus TRACHYCERAS, sensu stricto

TRACHYCERAS (TRACHYCERAS) sp.

Pl. 74, figs. 13–15

This subgenus is represented from the Natchez Pass formation of the East Range by two poorly preserved specimens that probably belong to the same species. The most complete specimen, though flattened and sheared ventro-dorsally, shows most of one side of the shell and about one-half volution of the venter. The other specimen is little more than a weathered cross-section, but a rim of silicified shell material projects above the matrix and shows some of the ornamentation. Both specimens show the row of double spines on each side of the ventral furrow that characterize the subgenus *Trachyceras*.

The original shape of the shell was discoidal and compressed with a fairly narrow umbilicus amounting to about one-fifth of the shell diameter. Ornamentation consists of closely-spaced, bifurcating, sinuous or

falcoid ribs, which extend from the umbilical shoulder to the median furrow on the venter, and which bear spines arranged in longitudinal spirals. Including the doubly-terminated spines bordering the ventral furrow, there are 10 rows of spines on either side of the whorl.

The suture is not exposed, and owing to the nature of preservation, shell measurements are not meaningful.

These specimens agree in general proportions, density of ribbing, and the number of spirals of spines with *Trachyceras* (*Trachyceras*) *desatoyense* Johnston from the Augusta Mountain formation of the New Pass Range, Nevada. Their preservation, however, precludes positive specific identification.

Figured specimens.—U. S. National Museum 130853 and 130854.

Occurrence.—U. S. Geol. Survey locality M777. Natchez Pass formation, East Range, Nevada.

Genus SPIROGMOCERAS Silberling, 1956
SPIROGMOCERAS SHASTENSE (Smith), 1904
Pl. 74, figs. 16,17

Trachyceras (*Protrachyceras*) *shastense* Smith, 1904, p. 391, pl. 46, figs. 9, 9a, pl. 48, figs. 3,4. Smith, 1927, p. 81, pl. 5, figs. 1–19.
Trachyceras (*Protrachyceras*) *lecontei* Hyatt and Smith, 1905, p. 194, pl. 44, figs. 1,2, pl. 45, figs. 1–9, pl. 46, figs. 1–15. Smith, 1927, p. 78, pl. 6, fig. 1, pl. 44, figs. 1,2, pl. 45, figs. 1–9, pl. 46, figs. 1–15.
Trachyceras (*Protrachyceras*) *beckeri* Smith, 1927, p. 79, pl. 4, figs. 1–8.
Trachyceras (*Protrachyceras*) *californicum* Smith, 1927, p. 79, pl. 1, figs. 1,2, pl. 2, figs. 1–7.
Trachyceras (*Protrachyceras*) *lindgreni* Smith, 1927, p. 80, pl. 3, figs. 1–6.
Trachyceras (*Protrachyceras*) *madisonense* Smith, 1927, p. 80, pl. 6, figs. 2–14.
Spirogmoceras shastense (Smith). Silberling, 1956, p. 1152.

Three external molds of partially crushed individuals showing the distinctive ornamentation of this species were found in the Natchez Pass formation in the northeastern hills of the Humboldt Range near Mill City.

The original compressed discoidal shape has been somewhat accentuated by crushing. Nevertheless, the flanks of the whorls, which increase in height rapidly, were evidently broadly rounded and graded gently into the narrow, evenly-rounded venter. Owing to the preservation the relative width of the umbilicus can only be estimated; it amounts to about one-fifth to one-fourth of the shell diameter.

The ornamentation is characteristic of this species and shows the distinctive and variable transition from finely tuberculate strigae to coarse projected ribs with strong and irregular tuberculation.

Typical specimens of this species, as expanded by Silberling (1956, p. 1148–1149), from Shasta County, California, have two different kinds of ornamentation according to their size and shell proportions. Compressed, relatively involute shells, like those included by Smith in *Trachyceras* (*Protrachyceras*) *lecontei*, have dominantly strigate ornamentation consisting of numerous spiral ridges of varying size which bear small tubercles corresponding in position to radial striae or fine ribs. More robust individuals, like Smith's *T.* (*P.*) *beckeri*, undergo an abrupt transition with increasing growth from this type of ornament to that consisting of coarse radial ribs, generally with some strigation and tuberculation on the venter bordering the narrow ventral furrow. The smaller of the two illustrated specimens from the Natchez Pass formation is a strigate variant; the larger specimen shows the transition to coarse radial ornamentation.

Traces of septa preserved on two of the specimens show that the saddles are complexly subdivided, but the complete suture line is not preserved. The largest specimen (not illustrated) is a completely septate phragmocone exceeding 110 mm. in diameter.

Figured specimens.—U. S. National Museum 130855 and 130856.

Occurrence.—U. S. Geol. Survey locality M265. Natchez Pass formation, northeastern Humboldt Range, Nevada.

Genus PARATROPITES Mojsisovics, 1893
PARATROPITES sp. cf. P. SULCATUS (Calcara, 1845, of Gemmellaro, 1904)
Pl. 74, figs. 5–11

Eutomoceras sulcatum (Calc.). Gemmellaro, 1904, p. 80, pl. 8, figs. 1–4, pl. 19, fig. 14.

This species is well represented by about 20 specimens that show most of the shell characteristics and by a greater number of fragmentary specimens preserved as external molds. These were studied by means of

latex rubber casts, which show a remarkable amount of detail.

Small individuals, less than about 40 mm. in diameter, are discoidal, but have moderately thick whorls equal to about one-half of their diameter. The greatest width is at the umbilical shoulder and the smoothly rounded flanks grade imperceptibly into the venter. With increasing size the shells become more compressed; on the largest uncrushed specimen the greatest whorl thickness is about 24 mm. which corresponds to a diameter of about 70 mm. The umbilicus is narrow and deep with a relatively constant width amounting to about one-tenth of the diameter.

Numerous narrow, flat ribs project forward and attain their greatest curvature as they approach the venter, on which they intersect the furrows bordering the ventral keel at an angle of about 30°. By repeated branching the ribs maintain a more or less constant density across the flanks as well as with increasing shell size. The average density is about 12 ribs/cm. measured along the spiral of coiling. The character of the flat, sharp cornered ribs, separated by relatively narrow interspaces, is the main reason for placing these forms in *Paratropites*. Owing to the forward curve of the flat ribs, their adoral edge is commonly slightly more elevated than the apicad edge, giving the ribbing a faint shingle-like aspect. The ventral keel is rounded, corresponds in width to one of the ribs, and does not project above the smooth curve of the venter. The narrow furrows bordering the keel are entirely within the shell material and are not impressed on the internal mold. The shell is devoid of tubercles or spiral striae.

Septa, shown at the adoral end of some specimens, have three prominent lateral saddles with ammonitic digitation.

These specimens from Nevada bear a strong resemblance to *Paratropites sulcatus* (Calcara) as illustrated by Gemmellaro (1904). They differ by having a slightly greater density of ribbing and by lacking the high, sharp ventral keel shown in some of Gemmellaro's figures. No other related species has such closely-spaced ribs. Gemmellaro assigned this species to *Eutomoceras*, a genus of Middle Triassic ceratites, as was customary until the genus *Discotropites*, with *Ammonites sandlingensis* Hauer as type species, was established for discoidal tropitids by Hyatt and Smith (1905). The typical species of *Discotropites* has ribbing and spiral striae like that of *Tropites*, sensu stricto. Discoidal forms like *P. sulcatus*, which show the *Paratropites* type of ornamentation, have generally been included in *Discotropites*, but it seems preferable to view the compressed shape as of secondary importance and to assign these forms to *Paratropites*.

Figured specimens.—U. S. National Museum 130858, 130859, 130860, 130861, and 130862.

Occurrence.—U. S. Geol. Survey locality M265. Natchez Pass formation, northeastern Humboldt Range.

Order NAUTILOIDEA

Genus PLEURONAUTILUS Mojsisovics, 1882

PLEURONAUTILUS? sp. cf. P. ALASKENSIS Kummel, 1953

Pl. 74, fig. 12

Pleuronautilus (p.) [sic] *alaskensis* Kummel, 1953, p. 34, pl. 4, figs. 5,6.

Two external molds showing the side of the shell and the umbilicus are comparable to the type specimen of this species. The flanks are flat and are separated from the venter and from the steep, convex umbilical wall by abrupt, angular shoulders. Very little of the venter is preserved, but it was probably broadly arched. The whorls were thus quadrangular in cross-section, and, judging from the depth of the umbilicus, somewhat wider than high.

Ornamentation consists of a prominent row of nodes along the ventro-lateral shoulder and along the middle of the flanks, and a less conspicuous row of nodes on the umbilical shoulder. On early whorls the lateral and ventro-lateral nodes apparently coalesce to form two continuous ridges. Radial ribs are only faintly suggested by swellings connecting the lateral and ventro-lateral nodes. More nodes are present on the ventro-lateral shoulder than on the flanks; on the orad half of the outer whorl about 13 ventro-lateral nodes correspond to about 8 lateral nodes. The greatest diameter of the illustrated incomplete specimen, is about 48 mm.; the corresponding width of the umbilicus is about 20 mm.

Compared with the holotype from Alaska, the Nevada specimens have more angular umbilical and ventro-lateral shoulders, fewer but more prominent lateral and ventro-lateral nodes, and more distinct nodes on the umbilical shoulder. Most of these differences can be attributed to preservation of the Nevada specimens as external molds whereas the holotype is wholly an internal mold. The Nevada specimens differ from typical representatives of *Pleuronautilus* in having nodes as the dominant ornamentation and in lacking well-defined radial ribs. In these respects the Nevada specimens and probably the holotype of *Pleuronautilus alaskensis* as well, are more like some species assigned to *Mojsvaroceras*. For example, the holotype of *M. turneri* Hyatt and Smith, which is a large partially unseptate whorl fragment with a row of lateral nodes and distinct umbilical and ventro-lateral shoulders, might represent the mature form of the relatively small shells referred to *Pleuronautilus alaskensis*.

Figured specimen.—U. S. National Museum 130857.

Occurrence.—U. S. Geological Survey locality M265. Natchez Pass formation, northeastern Humboldt Range, Nevada.

Class PELECYPODA
Genus SEPTOCARDIA
Hall and Whitfield, 1877
SEPTOCARDIA? sp.
Pl. 74, figs. 1–4

This pelecypod is represented by a large number of fragmentary specimens, most of which are disarticulated valves, preserved as both internal and external molds.

The complete shell is equivalved and strongly bi-convex with slightly opisthogyrate anterior beaks. The posterior and anterior aspect of the shell is heart shaped. The greatest width is at an abrupt change in the curvature of the valves along a line connecting the beaks with the posterior-ventral margin, so that in dorsal view the complete shell is more or less diamond shaped. In lateral view the valves are subtrigonal with a relatively short, smoothly rounded anterior margin and an abrupt, straight posterior margin nearly equal in length to the dorsal margin.

On the external surface about 32 V-shaped ribs radiate from the umbonal area. Closely-spaced concentric growth lines cross the ribs and are generally most pronounced in the interspaces between the ribs.

The hinge line is best shown by the internal mold of a right valve, a rubber cast of which is illustrated. A deep bean-shaped muscle-scar cavity, separated from the interior of the shell by a partition, is located near the anterior-dorsal margin. Between this cavity and the umbo is an elongate socket, which diverges slightly from the dorsal margin in an anterior-ventral direction. Beneath the posterior end of this socket and slightly anterior to the beak is a prominent cardinal tooth. Another small socket may have been located immediately posterior to the cardinal tooth, but it is not clearly shown because the posterior dorsal margin is poorly preserved. Remnants of a small posterior lateral tooth are present about midway between the beak and the posterior-dorsal margin. The position and orientation of the ligament groove is not shown by any of the specimens available. The partly preserved hinge line of a left valve has a prominent elongate tuberculiform posterior lateral tooth, separated by a groove from the dorsal margin.

The assignment of these specimens to *Septocardia* is necessarily tentative because the typical characteristics of this genus are subject to interpretation, as explained by Silberling (1959, p. 59–61). Briefly summarized, the difficulty in characterizing the genus *Septocardia* stems from the small, probably immature, nature of the type specimens of its typical species, *S. typica* Hall and Whitfield, described from Norian strata in the Clan Alpine Range, Nevada. Despite their small size these specimens are generally like those described here from the Natchez Pass formation in their shape and ornamentation and their hinge and muscle-attachment structures, but they apparently lack posterior lateral teeth. Larger specimens from the type locality of *S. typica*, however, have a well-defined posterior lateral tooth in the left valve. If these larger specimens are regarded as mature topotypes of *S. typica*, the generic name *Septocardia* is correctly applied to the shells described here and is a senior synonym of *Pascoella* Cox (1949), described from the Norian of Peru.

As provisionally redefined, *Septocardia* differs mainly in degree from *Paleocardita* Conrad (type species: *Cardita crenata* Goldfuss from the lower Karnian of the Alps); the anterior adductor scars of *Septocardia* are deeper, the posterior lateral teeth are better defined and tuberculiform, and the ligament groove is shorter and more oblique to the dorsal margin. These contrasting features are the same as those listed by Cox (1949, p. 34) that set his genus *Pascoella* apart from *Paleocardita*. The distinctions from *Paleocardita* in the specimens described here are not as extreme as they are in the Norian representatives of *Septocardia*, and the present specimens may be transitional between these two genera.

Figured specimens.—U. S. National Museum 130863, 130864, 130865, and 130866.

Occurrence.—U. S. Geological Survey locality M265. Natchez Pass formation, northeastern Humboldt Range, Nevada.

LOCALITY LIST

The following locality numbers used in the text are recorded at the Menlo Park, California, laboratory of the Paleontology and Stratigraphy Branch of the U. S. Geological Survey:

USGS loc. M265. Nevada. Pershing County. Imlay (15-min.) quadrangle. Southeastern Mill City Hills northeast of Nevada State Highway 50. At base of siliceous conglomerate, sandstone, and siltstone unit in overturned upper part of Natchez Pass formation. N. cent. SW¼, SW¼, sec. 9, T. 32 N., R. 35 E. Coll.: N. J. Silberling, Oct. 1958.

USGS loc. M657. Nevada. Pershing County. Humboldt Range. Buffalo Mountain (15-min.) quadrangle. Natchez Pass formation. Center of W½, sec. 13, T. 27 N., R. 34 E. Coll.: N. J. Silberling, 1956.

USGS loc. M777. Nevada. Pershing County. East side of East Range due east of Auld Lang Syne Peak. SE¼, sec. 7, T. 33 N., R. 37 E. Natchez Pass formation, about 400 feet above base and 100 feet below basic volcanic unit. Coll.: N. J. Silberling, Sept. 1957.

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SOME NEW FOSSIL TORTOISES FROM WESTERN NORTH AMERICA WITH REMARKS ON THE ZOOGEOGRAPHY AND PALEOECOLOGY OF TORTOISES

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ABSTRACT—The discovery of several fossil tortoises contribute significantly to our understanding of tortoise distribution in western North America. These include: *Gopherus neglectus*, n. sp. from the Oligocene part of the Sespe Formation, California; *Testudo milleri*, n. sp. from the Barstow Miocene of California; and *Gopherus depressus*, n. sp. from the Tehachapi Miocene of California. New material of previously known fossil tortoises is described.

A technique for the determination of past climates by the use of fossil reptiles and amphibians (Cowles and Brattstrom, MS: Brattstrom, 1956) and the temperature requirements of modern reptiles and amphibians assumes that the animals have not greatly changed their ecological requirements in the course of their evolution. One chance to test this assumption in one group of reptiles is afforded by the proximity (stratigraphically and geographically) of fossil plant and fossil tortoise sites. Some of the zoogeographic implications of the paleoecological data are discussed.

INTRODUCTION

FOSSIL tortoises (*Testudo*, *Gopherus*, *Stylemys*, etc.) are a difficult group with which to work. Most of the fossil species are known from fragments or, at the most, from single individuals, and rarely are the skulls, limbs, and shells intact. The problems involved in determining the conspecificity of any two isolated parts of even the better known forms is extremely difficult.

The similarity of the shell of tortoises in size, shape, and scutulation, results in the use of such characters as shell height, width, and length; scute and bone size and shape; and the positions of the various sulci or sutures for species determination. The more important characters in use for the determination of relationships among turtles are on parts not commonly found as fossils (skulls, cervical vertebrae, limbs, girdles). The amount of variation, scute abnormalities, asymmetry, and sexual differences present in living tortoises (Grant, 1936, 1946; Woodbury and Hardy, 1948) and the difficulty in separating even the living species of *Gopherus* (Bogert and Oliver, 1945), make the present classification of tortoises somewhat artificial. In spite of this, Williams (1950a, 1952, 1953) has greatly clarified the relationships of fossil tortoises and has presented classifications and phylogenetic trees of tortoises.

It is the purpose of this paper to place tortoises from several localities in western North America on record and to compare some of the Pleistocene *Gopherus* with their living relatives. In addition, some general speculations concerning the past distribution and paleoecology of tortoises will be discussed.

ACKNOWLEDGMENTS

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I wish to thank Drs. Thomas M. Oelrich and Ernest Williams for reading the manuscript and for their suggestions and criticisms.

SYSTEMATIC DESCRIPTIONS

EOCENE

?TESTUDO sp.

From the Eocene part of the Sespe Formation on the north side of Simi Valley, ventura County, California (Brattstrom, 1955; Stock, 1934) there are fragments of a large tortoise from several sites. The fragments

are unidentifiable as to species or genus, but are probably *Testudo* or "*Hadrianus*." This is the first record of a large tortoise from the Eocene of California and the first tortoise found in the Sespe Fauna. The specimens come from: C.I.T. Loc. 150[1] (two marginals of a large tortoise catalogued as C.I.T. 980), U.C. Loc. V5236 (=C.I.T. Loc. 143; consisting of fragments of a limb bone and fragments of a carapace), and U.C. Loc. V5242 (Brea Canyon, site 3, six fragments).

OLIGOCENE

GOPHERUS NEGLECTUS Brattstrom, n. sp.
Text-figs. 1–4

Holotype.—California Institute of Technology No. 126/1672 consisting of an entire shell except for the posterior one-fourth of the carapace (text-figs. 1,2).

Type locality and age.—C.I.T. Locality 126, Kew Quarry, Upper Oligocene part of the Sespe Formation, Ventura County, California.

Diagnosis.—A large *Gopherus* resembling *G. praeextans* and *laticunea* but differing from them in the shape of the neural bones and by having a broad, curved, not indented, anterior portion of the plastron. Nuchal scute broad; humeropectoral sulcus removed from entoplastron; pectoral scute broad, its median sulcus about one-half that of the abdominal. First neural elongate, quadrangular, second and third neural bone hexagonal.

Description of type.—The holotype (text-figs. 1,2) consists of a large, low, smooth, entire shell except for the posterior one-fourth of the carapace. It is badly smashed on top with the anterior-central region of the carapace depressed and pushed to the right so that three-fourths of the plastron is to the right of the mid-line of the carapace.

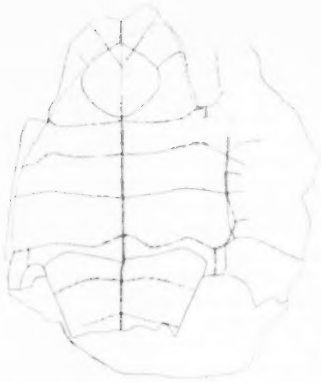
The epiplastron projects beyond the anterior edge of the carapace; carapace truncate with its anterior edge slightly indented and the anterior-lateral corners probably rounded. Nuchal scute (precentral) broad, wider than long. First neural elongate, quadrangular; second and third neural hexagonal. Plastron with gular-humeral sulci on entoplastron; humeropectoral sulcus not touching entoplastron; pectoral scute broad, not narrowing towards the mid-line and its median sulcus about one-half that of abdominal. Femoral scute broadly in contact with the inguinal and hence the abdominal scute does not touch the inguinal notch. Anterior-lateral edge of the plastron with a slight curve, not greatly indented at gular sulcus or epiplastron suture.

TEXT-FIG. 1.—*Gopherus neglectus* Brattstrom, n. sp. Dorsal view of carapace of holotype, LACM-CIT 126/1672. ×½

There is apparently an abnormality in the holotype in that the femoral scute appears to be divided on both sides into two scutes (see text-fig. 2).

Measurements of the holotype in millimeters are as follows: carapace length: 450; greatest width of carapace: 440; plastron length: 406; shell height: 151.8; length and width of central scute 1: 119.0 and 118.7; length and width of central scute 2: 94.0 and 100.6; length and width of proneural bone: 88.0 and 122.8; length and width of neural bone 1: 72.5 and 34.7; length and width of neural bone 2: 54.9 and 52.3; length and width of neural bone 3: 52.9 and 48.8; precentral scute (nuchal) length and width: 23.0 and 34.0. The length of the plastral scutes and bones at the mid-line are: gular 56.0, humeral 68.5, pectoral 50.3, abdominal 106.8, femoral 57.9, anal 65.2, entoplastron 99.2, hyoplastron 103.6, hypoplastron 81.6

[1] The Los Angeles County Museum has recently purchased the vertebrate paleontology collections of the California Institute of Technology. All C.I.T. numbers and localities listed herein should be preceded by L.A.C.M.



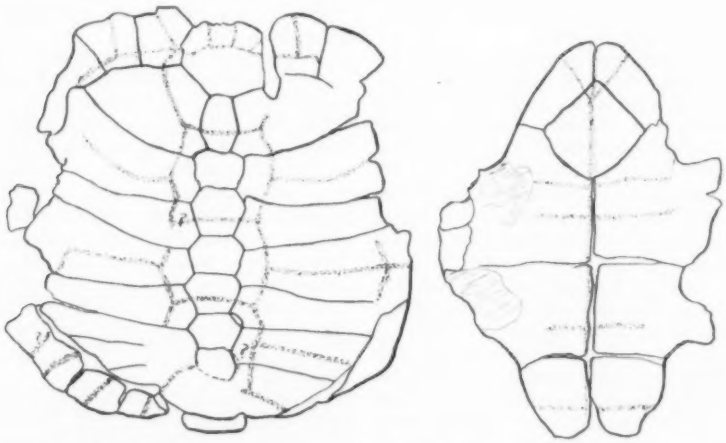
TEXT-FIG. 2—*Gopherus neglectus* Brattstrom, n. sp. Ventral view of plastron of holotype, LACM-CIT 126/1672. ×½

mm. The entoplastron width is 101.0 mm.

Referred material.—C.I.T. 126/1987 (text-figs. 3,4) from the same locality as the holotype consists of an entire shell. Only the plastron and part of the carapace is visible as the specimen is in an "*in situ*" display. The shell is badly broken so that the sutures and sulci are difficult to discern. The plastron has rounded anterior corners with no indentations at the gular sulcus or the entoplastron suture. The humeropectoral sulcus is not on or near the entoplastron. The median sulcus of the pectoral is broad and about half the length of the median sulcus of the abdominal. The xiphiplastron is notched behind. Measurements in millimeters include: plastron length 436.4; carapace length: approx. 450; carapace width: approx. 441.8; the mid-line sutures or sulci are: gular 36.9; humeral 121.0; pectoral 59.8; abdominal 123.9; femoral 77.4; anal 36.3; entoplastron 101.7; epiplastron approx. 123.8; hyoplastron ?96.5[2]; hypoplastron 121.1; xiphiplastron 74.0 mm. The entoplastron width is 114.4 mm. Pictures of this shell were apparently made prior to its utilization in the Museum display. These are presented in text-figs. 3 and 4.

Relationships.—*Gopherus neglectus* appears to be closely related to *G. praeextans* Lambe and *G. laticunea* Cope. It is most similar to the latter, especially in the shape of the anterior edge of the carapace and in the shape of the neural bones. *G. neglectus* differs from these two forms in the shape of the

[2] A question mark in front of a measurement in this paper indicates that it is for some reason (Ex. distortion of shell) an approximate measurement.



TEXT-FIG. 3—*Gopherus neglectus* Brattstrom, n. sp. Dorsal view of carapace of referred specimen, LACM-CIT 126z1987. Drawn from photograph. ×½.

TEXT-FIG. 4—*Gopherus neglectus* Brattstrom, n. sp. Ventral view of plastron of referred specimen, LACM-CIT 126/1987. Drawn from photograph. ×½.

neural bones and by having a broad, curved, not indented, anterior portion of the plastron. In this regard, *G. neglectus* has somewhat more primitive characters than *G. laticunea* in spite of the fact that it occurs in later beds.

The specific name, *neglectus*, is in allusion to the many fossil turtles (including this one) that remain on shelves, in storage, or even in full view (as with the referred specimen discussed above) for long periods of time unnoticed and unexamined.

MIOCENE

Additional tortoises from the Barstow Miocene of the Mohave Desert show that there is in addition to *Gopherus mohavense* Merriam, a *Testudo*. This new form is known from several specimens in the Los Angeles County Museum, one of which was referred to *G. mohavense* by Merriam (1919) when he described that species. By its characters (some of which were noted by Merriam) it cannot be *G. mohavense*. This specimen is designated the type of:

TESTUDO MILLERI Brattstrom, n. sp.

Holotype.—University of California, Museum of Paleontology, No. 21574 consisting of a shell.

Type locality and age.—Upper Miocene Barstow beds, Barstow syncline, San Bernardino County, California.

Diagnosis.—A medium-sized tortoise with the characters of the *T. tedwhitei* lineage of tortoises. Nuchal scute longer than wide, shell high and globular, anterior-lateral margins of carapace flared, nuchal indentation slight. Differing from *T. farri* in having the humeropectoral sulcus well separated from the entoplastron and the entoplastron just slightly wider than long. Differing from *T. ducatelli* and *farri* in having the gular region slightly distinct and having the medial sulcus of the pectoral scute about one-half that of the abdominal.

Description of type.—The holotype has been described and figured by Merriam (1919). The important characters are those of the diagnosis and: first central scute elongate, hexagonal; first neural hexagonal, second octagonal, third quadrangular; femoral scute not touching inguinal scute, hence abdominal scute enters the inguinal notch. Measurements of the type are given by Merriam (1919) and in Table I.

Referred material.—C.I.T. 494/5129 (text-figs. 5,6) from the south limb of the Barstow syncline (in S.W. corner, N.W. ¼, S.E. ¼, Sec. 15, T11N, R2W, SBB&M) consists of the anterior half of a tortoise. Most of the bones and scutes are discernible except on the mid-lateral areas of the carapace and the lateral areas of the plastron. The characters are similar to that of the type, the most important of which include the elongate nuchal, entoplastron wider than long, the high, dome-shaped shell, and the elongate central scute one.

C.I.T. 495/5130 from the south limb of the Barstow syncline, ¾ mi. S.E. of locality 494 and 100 feet above it stratigraphically (approximately in the middle of the N½, SW¼, Sec. 14, T11N, R2W, SBB&M) consists of a complete shell. The carapace is badly smashed and the central portion is missing. The last suprapygals are present but damaged. The plastron is also badly cracked so that only the posterior one-third and parts of the epiplastron and hyoplastron are evident. Enough of the shell is present so that certain characters allow for its placement here. Measurements of these last two specimens are given in Table I.

U.C. 21573 used by Merriam (1919) in his definition of *G. mohavense*, is unidentifiable at present.

Discussion.—The characters of *Testudo milleri* all suggest a relationship with the *T. tedwhitei* lineage of *Testudo* as defined by Williams (1953). *T. milleri* differs from members of that group by having the medial sulcus of the pectoral scute about one-half that of the abdominal and by having the gular region slightly distinct. *T. milleri* differs from the Upper Miocene, *T. farri* in having the humeropectoral sulcus well separated from the entoplastron and in having the entoplastron just slightly wider than long. Perhaps both *B. farri* and *milleri* are derivatives of the Middle Miocene *B. ducatelli*.

Though the characters of the species place *milleri* in the *tedwhitei* line of *Testudo*, one of the characters of the species does not conform with this lineage or even with the genus *Testudo*. Williams (1953) has suggested that a small inguinal scute, not touching the

TABLE 1—MEASUREMENTS IN MILLIMETERS OF SEVERAL SPECIMENS OF *Testudo milleri*. THOSE OF THE TYPE SPECIMEN TAKEN FROM MERRIAM (1919)

Character	Type UC 21574	CIT 494/5129	CIT 495/5130
Carapace length	—	?360.0	334.5
Carapace width	317.0	?329.2	?209.5
Plastron length	?375.0	—	339.2
Shell height	—	170.8	149.5
Central scute 1, L.	83.0	88.5	—
Central one, W.	82.5	76.2	—
Neural one, L.	48.0	39.6	—
Neural one, W.	39.0	?36.6	—
Nuchal scute, L.	26.5	27.2	—
Nuchal scute, W.	18.2	19.7	—
Proneural length	72.0	82.5	—
Proneural width	90.0	89.0	—
Gular length	—	73.8	?55.0
Humeral length	74.0	68.1	—
Pectoral length	46.5	44.2	—
Abdominal length	81.5	—	—
Femoral length	46.5	—	52.7
Anal length	50.0	—	?27.8
Entoplastron length	73.0	73.4	—
Hyoplastron length	93.0	95.5	—
Hypoplastron length	70.0	—	68.9
Xiphiplastron length	82.0	—	71.4
Entoplastron width	—	81.9	—

femoral is one of the diagnostic characters of the genus *Stylemys*. The femoral scute does not touch the inguinal in *T. milleri*. This may be a specific characteristic of *milleri* or *milleri* may be, in fact, an extension of the *Stylemys* line into the Miocene.

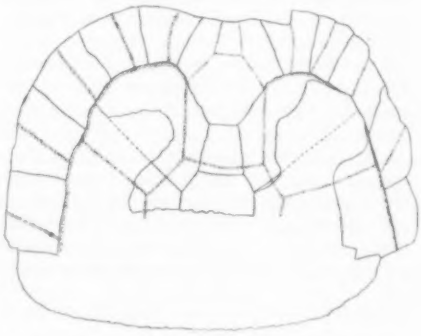
The species is named in honor of Dr. Loye Miller who first identified birds from the Barstow beds (In Merriam, 1919), who has contributed greatly to our knowledge of avian paleontology, who has added much to the natural history and behavior of the modern desert tortoise (Miller, 1932, 1955), and who has stimulated the interest of many students.

GOPHERUS MOHAVENSE Merriam

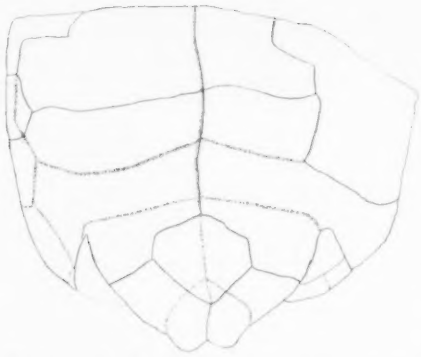
Referred material.—C.I.T. 494/5131 from the Barstow syncline consists of fragments of the plastron, carapace, and pectoral girdle. They represent a large tortoise, but appear to be referrable to *G. mohavense* (Ex. nuchal scute wider than long). Measurements made on this material in millimeters includes: entoplastron length 78.3; entoplastron width 96.9; length and width of central scute one: 92.2 and 102.4; precentral scute length and width: 22.0 and 29.1 mm.

U.S.G.S. 473, Barstow syncline, consists of several fragments. The length and width of the entoplastron included are: 45.5 and 50.0 mm.

L.A.C.M. A1420, Barstow syncline, consists of a mold of a shell with the bones of the plastron present. It is a low turtle with the plastral characters of *G. mohavense*. The lengths of the plastral bones and scutes at the mid-line are: gular ?21.0; humeral 32.3; pectoral 13.9; abdominal 44.6; femoral ?22.8; anal ?6.0; epiplastron ?38.0; ento-



TEXT-FIG. 5—*Testudo milleri* Brattstrom, n. sp. Dorsal view of carapace of referred specimen, LACM-CIT 494/5129. ×½.



TEXT-FIG. 6—*Testudo milleri* Brattstrom, n. sp. Ventral view of plastron of referred specimen, LACM-CIT 494/5129. ×½.

plastron 46.6; hyoplastron 39.8; hypoplastron 44.9; xiphiplastron ?17.0. The entoplastron width is 45.3; carapace length ?202.0; greatest width of carapace ?164.8; plastron length 174.0; shell height ?78.6 mm.

C.I.T. 303/5132, Tejon Hills, Kern County, California, consists of the anterior and posterior parts of a plastron which are similar to *G. mohavense*. The gular-humeral sulci turn as they approach the intergular sulcus so that they meet that sulcus at right angles and not diagonally as in *G. mohavense*. The mid-line measurements of this turtle are: gular 68.0; epiplastron 51.5; anal ?46.4; femoral 22.7; xiphiplastron 53.0 mm. The entoplastron width is ?91.7. The age of this deposit at C.I.T. locality 303 is probably Upper Miocene (See Drescher, 1941, for a discussion).

The Tejon Hills locality of *Gopherus mohavense* is on the opposite side of the southern Sierra Nevada-Tehachapi Mountain Range from the Barstow syncline. The occurrence of the same species of tortoise on opposite sides of this range in the Upper Miocene suggests, along with paleobotanical and geological evidence (Axelrod, 1950d, 1956), that this mountain range was probably not very high in Upper Miocene times.

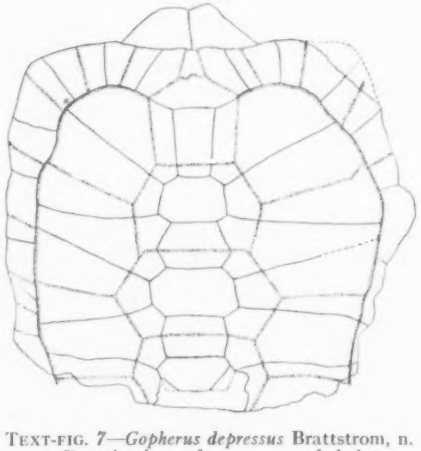
GOPHERUS DEPRESSUS Brattstrom, n. sp.
Text-figs. 7,8

Holotype.—California Institute of Technology No. 498/5133, consisting of the entire shell of a tortoise.

Type locality and age.—C.I.T. locality 498, Bopesta formation, Cache Peak fauna, Tehachapi Upper Miocene, West ½, N.E.¼, sec. 36, T. 31S, R34E, MOB&M, Tehachapi Mountains, Kern County, California. The specimen was collected by R. H. Tedford and R. L. Schultz from their locality V494. The locality encompasses a basin to the north of the "South" Fork of Cache Creek.

Diagnosis.—A low, flat tortoise similar to *G. mohavense* (from which it differs in being depressed; in having neural bone one widest anteriorly and not posteriorly; neural bones three and five hexagonal rather than quadrangular; the entoplastron wider than long), and the depressed *G. pansa* (from which it differs in being more depressed, larger, in having the anterior edge of neural one widest, and in having the entoplastron wider than long). Anterior-lateral corners of carapace rounded; nuchal indentation not marked; humeropectoral sulcus separated from entoplastron; nuchal scute about equal in length and width; first neural bone elongately quadrangular, second octagonal, third hexagonal, fourth octagonal, fifth hexagonal.

Description of type.—The holotype (text-figs. 7,8) is low and flat with a carapace length and width of 315.0 and 327.2 mm. respectively. The shell height is 108.9 mm. The nuchal scute is just a little wider (19.6



TEXT-FIG. 7—*Gopherus depressus* Brattstrom, n. sp. Dorsal view of carapace of holotype, LACM-CIT 498/5133. ×½.

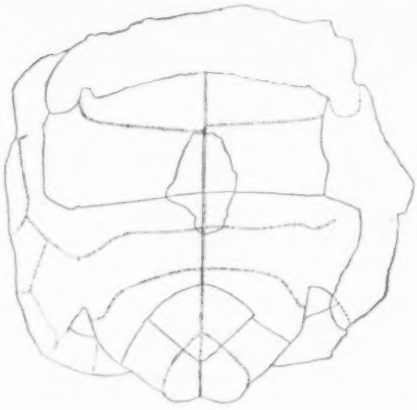
mm.) than long (18.0 mm.). The first central scute is hexagonal with the central-nuchal margin wavy; central scutes 1 to 4 wider than long and all hexagonal; proneural wider than long (88.3×48.4 mm.); neural one elongate, quadrangular, with its anterior end wider than its posterior end; neural two and four octagonal; neural three and five hexagonal. The anterior margin of the shell is somewhat truncate, with only slight nuchal indentation and with rounded anterior-lateral corners. The anterior edge of the plastron is rounded with only a slight indentation at the gular-humeral sulcus. The humeropectoral sulcus is removed from the entoplastron and the median sulcus of the pectoral is about one-third that of the abdominal. The mid-central portion of the abdominal is missing in the holotype. The entoplastron is wider than long and is somewhat triangular with the posterior margin gently curved.

Measurements include: length and width of centrals; one: 69.9–73.2; two: 68.3–98.9; three: 70.6–121.8; four: 71.0–106.0; length and greatest width of neurals: one: 54.0–33.7 (posteriorly the width is 26.9); two: 34.5–52.6; three: 37.0–59.6; four: 36.3–63.2; five: 30.3–49.6; six: 30.0–?62.5. The length at the mid-line of the plastron scutes and bones: gular 56.3: humeral 50.9: pectoral 32.2; abdominal 79.6; epiplastron 32.6; entoplastron 63.7: hyoplastron 73.0; hypoplastron ?97.0 mm. The entoplastron width is 81.5 mm.

Relationships.—*Gopherus depressus* appears to be closely related to *G. mohavense* and *G. pansa*. *G. depressus* differs from these two forms in having the shell more compressed, in having the anterior edge of neural one wide anteriorly and not posteriorly, and in having the entoplastron wider than long. *G. pansa* and *G. depressus* occur in beds of about equal age (Galbreath, 1953; Buwalda, 1916; Wood, 1941) and are probably most closely related. Perhaps *G. pansa*, *depressus*, and *mohavense* are all derived from some more primitive form such as *G. vaga*.

STYLEMYS CONSPECTA Hay

Referred material.—Several tortoises, all from the John Day Miocene of Oregon, are present in the collection of the University of California at Berkeley and are probably of this species. These include entire shells,



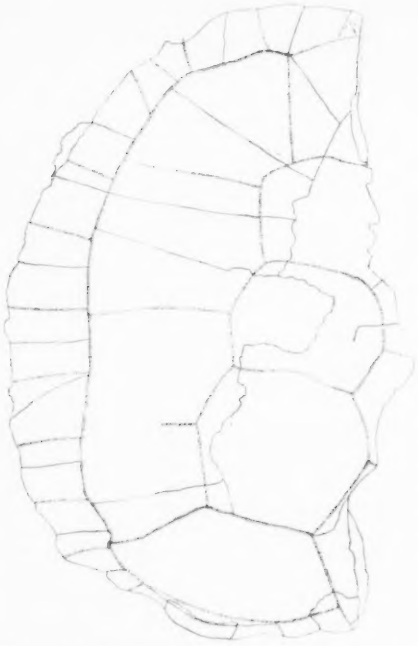
TEXT-FIG. 8—*Gopherus depressus* Brattstrom, n. sp. Ventral view of plastron of holotype, LACM-CIT 498/5133. ×½.

fragments, and coprolites from localities 818, 847, and 827. Two shells in the California Institute of Technology collection from the E.N.E. end of Haystack Valley, Oregon also seem to be *S. conspecta*. An additional C.I.T. specimen (1/1731 from the Middle John Day of Sheep Mountain, Oregon) is similar to the Kew Quarry *Gopherus neglectus*, but unfortunately it is so damaged as to prevent checking this suggestion.

PLIOCENE

As Williams (1950a) notes, Pliocene tortoises are quite numerous, but almost all are known from fragments and most are unassignable generically. The Pliocene material to be listed or discussed below is cited primarily to add geographic records of fossil tortoises for purposes of the paleoecological and zoogeographic discussions presented later in this paper.

C.I.T. locality 448, Yepomera (= Rincon) Formation, Chihuahua, Mexico, Upper Pliocene. From this locality there is a very large tortoise (carapace length 711.0, carapace width ?636.0, shell height 235.0 mm.) represented by the left half of the carapace (Fig. 9) and plastron. The plastron is too damaged to recognize any sutures or sulci. The length and width of the central scutes are: one: 132.6×?; two: 121.7×?; three: 120.8×170.4; four: 165.2×183.0; five: 144.7×254.0 mm. respectively. The



TEXT-FIG. 9—Dorsal view of carapace of tortoise from Pliocene Yepomera Fm., Mexico. ×¼.

postcentral scute is 63.7 mm. long and 98.6 mm. wide. The proneural is approximately 119.3 mm. long and 150.0 mm. wide. The general shape (low and depressed, anterior-lateral corners of carapace curved, fourth central scute wider than long) suggest that the specimen is probably a *Gopherus*. The material is lacking, however, in the diagnostic characters for proper generic and specific determination.

L.A.C.M. locality 1111 (Ted Downs locality 416), Vallicitos area, eastern San Diego County, California, Pliocene. Two tortoises from this locality are represented by 19 fragments including two parts of (a?) xiphiplastron (anal scute length of the two pieces: 41.5 and 41.8 mm.). The material represents a large tortoise.

C.I.T. locality 162, Rio Virgines, Nuevo Leon, Mexico, Pliocene. From this locality there is a part of the shell of a very large tortoise.

C.I.T. locality 486, Hungry Valley Formation, Late Pliocene, S.E. ¼, Sec. 21, T8N, R18W, Ft. Tejon Quad. Los Angeles County, California. Two fragments of bone of a large tortoise from this locality are undeterminable as to species.

U.C. V3721, Cita Canyon, Randall County, Texas, Late Pliocene. Several specimens from the Cita Canyon area in the collection of the University of California include: 43274 (C.W.T. 2623), consisting of the anterior part of a plastron that is very similar to modern *Gopherus*. The mid-line measurements include: gular: 31.0; humeral 24.5; pectoral 11.0; epiplastron 21.3; entoplastron 36.6; hyoplastron 28.1; entoplastron width 37.5 mm. Another entoplastron (C.W.T. 1207) measures 40.7 mm. long and 39.6 mm. wide. Number 43294 consists of the posterior part of a plastron of a large tortoise. The length of the xiphiplastron of this specimen is 104.3 mm. J.W.T. 2275 consists of several fragments of shell, a cervical vertebra, a femur, and an egg (the latter measures 49.5×48.2×46.9 mm.). Cita Canyon is the locality of *Gopherus canyonensis* (Johnston) and near the Blanco localities of *T. turgida* (Cope) and *G. campester* (Hay), (Williams, 1950a; Johnston and Savage, 1955; Oelrich, 1957).

U.C. V5125, Cammatte Ranch, San Luis Obispo County, California, Clarendonian Pliocene includes four fragments (U.C. 40970) of a large tortoise.

U.C. V3322/33528, Big Spring Canyon, Bennet County, South Dakota, Clarendonian Pliocene, consists of fragments of a tortoise.

U.C. V1751/29279 (many fragments) and V1083/29280 (one fragment) come from the Ricardo Beds, Kern County, California, Clarendonian Pliocene.

U.C. V4845/GB 525, Brady pocket, Churchill County, Nevada, Pliocene, includes many fragments of tortoise.

U.C. V3952/36080, ¼ mi. S. Ingram Creek, Stanislaus County, California (S.W. ¼, N.E. ¼, Sec. 2, T 4S, R6E), Lower Pliocene consists of many fragments of the shell and limbs of a very large tortoise.

U.C. V2824/30306, Lipscomb County, Texas, Lower Pliocene, consists of a large fragment of a tortoise.

U.C. 23417 and 23418, San Timoteo

Formation, San Timoteo Canyon, Riverside County, California, Upper Pliocene. These tortoise fragments were recorded by Frick (1921).

PLEISTOCENE

Most of the Pleistocene tortoises can be referred to living species. There are in addition several species of gigantic tortoise living in the Pleistocene. The Pliocene and Miocene ancestors of many of the Pleistocene and recent tortoises are unknown. This is largely due to the lack of adequate Pliocene material.

Species of the living *Gopherus* are difficult to distinguish. They are geographically separated and are considered as species by most herpetologists. Mertens (1956), however, has considered the three living forms of *Gopherus* as subspecies. In general, *G. berlanderi* is small and rugose with deep growth lines on the scutes. The pygal is usually turned ventrally. The anal and pygal almost encircle the tail. *G. polyphemus* is large, low, and usually has a smooth carapace. *G. agassizi* is somewhat intermediate in these characters between *berlanderi* and *polyphemus*. The variation in each of the species is so great, however, that given a number of individuals, it is almost impossible to separate them into their proper species on the basis of shell characters. Skull characters (Bogert and Oliver, 1945; Williams, 1950a, 1952) appear to be the only reliable criteria available for distinguishing the species. Skulls, of course, are rare as fossils.

G. polyphemus and *agassizi* are known from Pleistocene specimens that do not differ greatly from Recent specimens. The following includes additional records or material of *G. agassizi*.

GOPHERUS AGASSIZI (Cooper)

L.A.C.M. locality 1010, Shelter Cave, New Mexico, Late Pleistocene. From this cave there are many fragments of tortoise that do not differ from *G. agassizi*. Many of the tortoise bones are burned, probably by Indians that had inhabited the cave. This and the following locality are far outside the present range of *G. agassizi*. The specimens do not resemble *berlanderi*, other than being generally smaller than average *agassizi*. As most of the bones are isolated, there is no standard (Ex. plastron length) for comparison with recent *G. agassizi*. Some measurements on isolated elements include: Length gular scute at mid-line: 33.0, 41.9, 31.3, 33.0, 34.8, 44.6, 28.7, 23.8, 31.8 mm.; length humeral at mid-line: 48.8, 44.8 mm.; length of entoplastron: 36.7, 40.0, 50.5. mm. In all individuals the precentral scute is wider than long.

L.A.C.M. locality 32–35, Conkling Cavern, New Mexico, Late Pleistocene. Fragments of shell from this cave are similar to *G. agassizi*.

L.A.C.M. locality 1123, Schuiling Cave, San Bernardino County, California, Late Pleistocene. There are shell and limb fragments in this cave deposit from a depth of a few inches to 15 feet. One specimen (L.A.C.M. 1534) consists of a partial carapace. The measurements on this carapace do not differ from Recent *G. agassizi* (length and width of central scutes: one: 65.1–71.2; two: 55.5–86.6: three: ?62.0–?91.8; length and width of neurals: one: 40.5–27.5; two: 27.3–47.7; three: 25.0–39.0 mm.

U.S.G.S. locality: Lower portion of Manix beds, Manix Dry Lake, San Bernardino County, California, Pleistocene. Mr. Herb Winters sent the writer a coracoid and a marginal from the Manix beds for identification. Some of the measurements of the caroacoid are: greatest length 38.9; greatest width 31.7; greatest width anterior end 16.0; greatest width posterior end 9.4; thinnest part 4.6 mm. The marginal measures 21.5 $\times$20.2 mm. in length and width is 6.4 mm. thick. The marginal is undiagnostic. The coracoid is similar to recent *G. agassizi*, but is heavier in that the distal and medial ends are thicker than in the modern species.

C.I.T. locality: Gypsum Cave, Nevada, Late Pleistocene. The Gypsum Cave *Gopherus agassizi* were reported on by Harrington (1933) and Brattstrom (1954). Measurements made on this and other Pleistocene material were compared with Recent *G. agassizi* on some 18 different graphs. In general there was either a close agreement between the modern and Pleistocene forms (carapace length plotted against shell height, gular length-humeral length, plastron length-anal length, plastron length-hypoplastron length, and plastron length-xiphiplastron length) or the scatter of the

recent or fossil measurements was so great as to prevent any tendencies from being evident (entoplastron length and width, gular length-plastron length; plastron length-femoral length; entoplastron length-humeral length). In several characters (nuchal scute length and width, abdominal length-plastron length, hyoplastron length-plastron length, pectoral length-plastron length, entoplastron length-plastron length, epiplastron length-plastron length, carapace length-shell width) there were slight differences between recent and Gypsum Cave specimens. In the Gypsum Cave material 4 out of 7 entoplastrons had no gular sulci on them. This may be a sexual character, however, with males lacking gular sulci on the entoplastron and females and young (?) having gular sulci on the entoplastron. This needs to be checked, however, with a large series of recent *G. agassizi*.

Measurements made on fossil *G. agassizi* were plotted on the growth record graphs of living *G. agassizi* made by Miller (1955). These graphs show no differences between fossil and Recent *G. agassizi* with regard to carapace length and width.

PALEOECOLOGY

Many workers have used the occurrence of fossil tortoises to suggest the past climates of a given fossil locality. They have generally assumed that the presence of tortoises is indicative of arid conditions (cf. "the desert tortoise," *Gopherus agassizi*) and we find such statements as, " . . . The presence of large tortoises is possibly to be correlated with open semi-arid character of the country." (Merriam, 1919, Barstow Miocene). It will be shown below that most fossil tortoises are, in fact, probably indicators of tropical and subtropical climates.

CLIMATIC DISTRIBUTION OF MODERN TORTOISES

The following genera or subgenera of tortoises are entirely or primarily tropical (text-fig. 10) in distribution: *Testudo* (*Chelonoidis*), South America and Galapagos Islands; *T.* (*Asterochelys*), Madagascar, Aldabra, Seychelles; *T.* (*Cylindraspis*), Rodriguez and Mauritius; *T.* (*Acinixys*), Madagascar; *T.* (*Psammobates*), Africa; *T.* (*Malacochoersus*), Africa; T. (*Geochelone*), Asia, Africa; *T.* (*Manouri*), Asia; *T.* (*Indotestudo*), Asia, East Indes; *Kinixys*, Africa; *Homopus*, Africa; *Chersina*, Africa; *Bellemys*, Madagascar (classification from Williams, 1950a; habitats from Gadow, 1909; Smith, 1931; Schmidt, 1919, etc.). (Williams, (personal communication), says that *Homopus*, *Chersina*, and *T.* (*Psammobates*) are primarily South Temperate.) Most of these forms occur in tropical jungles, forests, or savannas, most often in open areas in these habitats. There may be marginal species of a few of the groups mentioned above that occur in sub-tropical regions.

The tortoises of the Galapagos Islands are (and were) apparently much more abundant on the higher elevations of the various islands where tropical conditions occur than on the lower, semiarid slopes where the Iguanas occur (Slevin, 1931; Darwin Voyage of the Beagle; plus personal reports to the writer on several recent photographic expeditions to the islands).

The modern European and Asiatic tortoises, *Testudo* (*Testudo*), occur primarily in warm mediterranean or subtropical climates (Gadow, 1909).

The climatic distribution of the modern *Gopherus* is not too dissimilar from that of *T.* (*Testudo*). *Gopherus polyphemus* of the humid subtropics (Visher, 1954, maps 981–983, 985–987) of the southeastern United States is a characteristic animal of the high pine woods in peninsular Florida (Carr, 1950, 1952). Its occurrence in sandy ridge and dune-sand areas appears to be associated with the requirement of having to burrow above the water table (Carr, *supra cit.*).

Gopherus berlandieri occurs in subtropical regions (according to the classification found in Visher, 1954, maps cited above) of southern Texas and northeastern Mexico. According to Carr (1952) it is, " . . . perhaps partial to open woods, it is found also in chaparral and mesquite. . . . "

Gopherus agassizi is primarily a desert dweller. It does not occur in the low, hot Colorado desert, but rather in the high Mohave Desert of California and in the high deserts of Nevada, Arizona, and Utah. This area is classified (Visher, 1954, maps 982, 987) as dry subtropical. In the Alamos region of Sonora, *agassizi* is found in a

xerophytic thorn-scrub or chaparral type of vegetation (Bogert and Oliver, 1945). The latter is the plant type that until recently (U. Pliocene) covered the Mohave Desert (Axelrod, 1950d).

BEHAVIOR OF MODERN TORTOISES WITH REGARD TO CLIMATE

The modern species of *Gopherus*, save possibly *G. berlandieri*, typically burrow into the ground. These burrows are resorted to during the winter and the hot parts of the summer (Woodbury and Hardy, 1948; Miller, 1932, 1955). The Mediterranean forms, *Testudo* (*Testudo*), burrow in the winter. Several of the tropical or subtropical tortoises that live in open areas burrow during the dry or non-rainy season (Gadow, 1909). Those tortoises in the dense tropics and the gigantic tortoises of the Galapagos and Indian Ocean Islands do not burrow. Supposedly the large fossil species also did not burrow.

The burrows are primarily, if not entirely, for the avoidance of extremes of temperature (Woodbury and Hardy, 1948) and where there are no great temperature hazards, the forms do not burrow. For example, Bogert and Oliver (1945) observed that *G. agassizi* which is known for its burrowing activity in the Mohave Desert region, does not burrow in the equable climate of the Alamos region of Sonora. Because of their burrowing behavior and avoidance of climatic extremes, the burrowing populations of tortoises, while active, are essentially living in a subtropical climate. For example, *G. agassizi* is active in the Spring and sometimes in the Fall when the Mohave desert is warm and equable and the vegetation is in bloom.

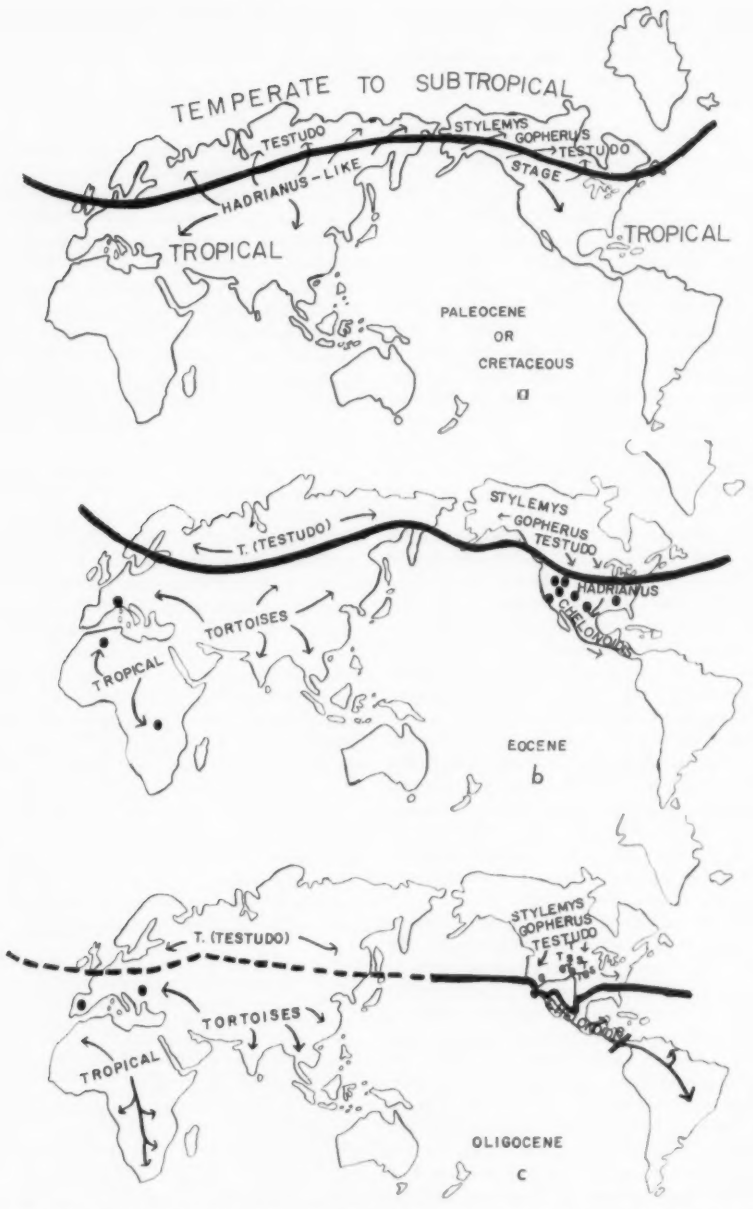
Modern tortoises are almost entirely herbivorous, preferring succulent foods. In tropical and subtropical regions such foods are almost always available to the tortoise. In areas where there is a marked seasonal rainfall and succulent food is available only during a certain time of the year, the tortoises are burrowers and emerge from their burrows only when the climate is suitable and the succulent food is available. For example, *G. agassizi* is most active in the Spring and somewhat active in the Fall when the desert flowers are in bloom and the leaves are present on most of the plants. Contrary to popular belief, *G. agassizi* apparently does not eat cacti which are available all the year.

TEMPERATURE REQUIREMENTS OF MODERN TORTOISES

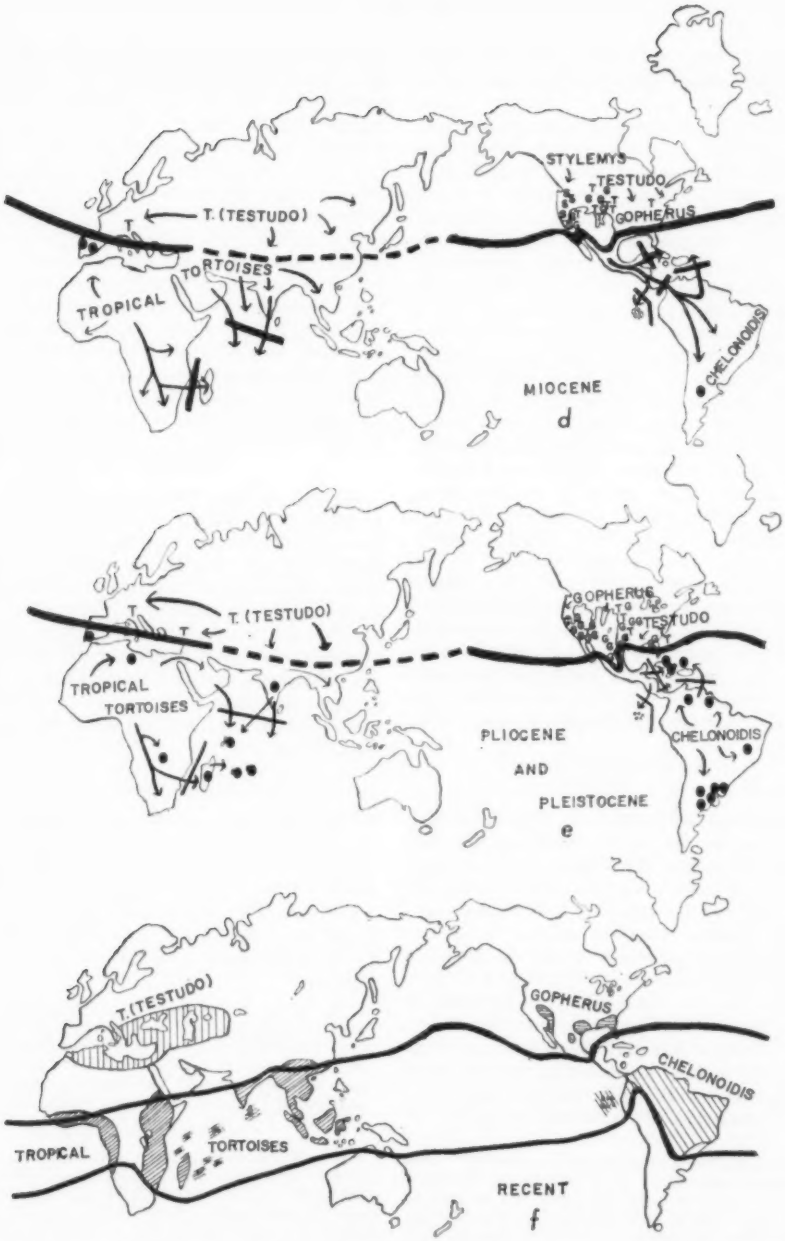
A review of the temperature requirements of modern reptiles and amphibians has been given by Cowles and Brattstrom (MS). For *Gopherus agassizi* they showed that active individuals (*i.e.* not those in burrows which had body temperatures of 10.0° to 22.0°C.) had body temperatures that ranged from 19.0°C. (the minimum voluntary) to 37.8°C. (The maximum voluntary) with a mean or preferred temperature of 30.6°C. The critical maximum for this species is 39.5°C. and the lethal is 43.0°C. The preferred body temperature of *G. polyphemus* is 34–35°C. according to Bogert and Cowles (1947).

Since tortoises are dependent primarily upon solar radiation and conduction from the substrate for their source of body heat (*i.e.* there is no internal mechanism for heat production: see Cowles and Brattstrom, *supra cit.*), and since small tortoises absorb heat faster than large tortoises, the presence of gigantic tortoises in more northern latitudes than today (Ex. Kansas in the Pliocene, Montana in the Miocene, Wyoming in the Oligocene, etc.) suggests that the climates were much warmer and more constant then.[3] If it were not equable throughout the year and if at least partial shade in the form of a forest were not available, then these large tortoises probably could not have existed. Without mild, equable climates and shade the large tortoises, which more than likely did not burrow, would probably have absorbed too much solar radiation and reached their lethal temperatures. If it were

[3] It should be apparent that the tropics are not hotter than deserts or semideserts, but are characterized by having relatively constant temperatures throughout the year. It is in desert (and some subtropical) regions that the high extremes of temperatures are reached and the general climate is variable. Compare, for example, the minimum and maximum temperatures recorded for areas in the tropics: Barbados, 61–90; Bombay, 56–100; Colombo, 62–97; Cristobal, 66–90; Guam, 67–94; Singapore, 66–97°F. with those recorded in arid regions: Cairo, 31–112; Karachi, 40–118; Los Angeles, 28–109; Tunis, 30–118; Death Valley, 15–134°F. (Data from Tannehill, 1943; Putnam, 1947).



TEXT-FIGS. *10a–f*—Maps showing changes in distribution of fossil tortoises associated with changes in past climates as determined from paleobotanical data. Transcontinental solid line separates tropical from Subtropical to warm temperature areas. Short solid lines represent oceanic barriers.



Solid circles: tropical tortoises including: *Achilemys; Cymatholcus; Chelonoidis; Hadrianus; Monachelys.* Letters: temperature to subtropical tortoises including: *S, Stylemys; T, Testudo (Testulo)* or *Testudo (Hesperotestudo); G, Gopherus.*

too cool, they probably could not have absorbed enough heat to allow them to be active.

In regard to burrowing forms, the activity of the modern *Gopherus agassizi* (as studied by Woodbury and Hardy, 1948; Miller, 1932, 1955; Grant, 1936, 1946; and the writer) is illustrative. In the Spring it is active in the morning. By noon it crawls into the shade of a bush or rock, often scooping out a small cavity or depression for shade. By mid or late afternoon the turtle again becomes active. At night it returns to its noon-type of resting spot or to its burrow. In early Summer with more intense solar radiation and lack of great loss of heat from the ground at night, the time of activity of the tortoises is greatly shortened, (early in the morning, for an hour at most, and another short period in the late afternoon). Mid-summer finds the tortoises "aestivating" in burrows where temperatures are lower (approximately 20°C.) than the lethal temperatures of the outside environment. In the Fall there is a period of activity similar to that in the early Summer.

The Winter finds the tortoises deep in their burrows or dens where temperatures are mild (10–20°C.) while the outside environment may reach freezing temperatures.

CLIMATIC DISTRIBUTION OF FOSSIL TORTOISES

A technique for the determination of past climates by the use of fossil reptiles and amphibians and the temperature requirements of modern reptiles and amphibians (Cowles and Brattstrom, MS; Brattstrom, 1956) assumes that the animals have not greatly changed their ecological requirements during the course of their Cenozoic evolution. For example, if an ectotherm[4] occurs primarily in the tropics, it is suggested that it has probably been in tropical areas for most of its evolution—or that part of its evolution in which that particular taxa is recognizable. By plotting the fossils of known climatic preference backwards in time, we can use this data, provided it conforms with the paleobotanical data, to suggest past climates.[5] A chance to test this assumption in one group of Reptiles is afforded by the proximity (stratigraphically and geographically) of fossil plant and fossil tortoise sites. Examination of the paleobotanical reports from the vicinity of tortoise deposits shows that tropical tortoises have apparently always lived in tropical areas and subtropical tortoises have generally lived in regions of a subtropical nature. The floras discussed below are fully elaborated upon in each of the papers mentioned, in references found in the papers cited, or are listed in Knowlton, 1919; or La Motte, 1944.

EOCENE

Several of the Eocene floras (Clarno, Jackson, Green River, Wind River, Yellowstone, Wasatch, and to a lesser extent La Porte, Comstock, Chalk Bluffs, Claiborne; MacGinitie, 1941) occur stratigraphically and geographically near sites of tortoise collections (Williams, 1950). The distribution of these floras and the distribution of fossil Eocene tortoises (text-fig. 10) suggests that most, if not all, of the Eocene tortoises were tropical or slightly subtropical in distribution.

OLIGOCENE

A humid, warm-temperate to subtropical fossil flora with seasonal change in rainfall is well known from the Lower (or Lower and Middle) Oligocene Florissant beds of Colorado. In all, some 114 species are accurately known from this flora. MacGinitie's (1953, p. 77) conclusions as to the ecology of the flora are,

> "The Oligocene forest occupied streamside and lakeside habitats in a piedmont of low relief and moderate elevation which bordered the Rocky Mountain uplift on the east. The drainage was disorganized and partly ponded by successive volcanic outbursts which covered the area with dust, pumice, and mud-flows.

[4] Ectotherm: a more accurate name for "cold-blooded vertebrates" or poikilotherms. It refers to the source of heat, *i.e.* from the outside in contrast to the endotherms (birds and mammals) where heat is generated internally (See Cowles, 1945).

[5] If no fossils of reptiles are available, we can use this assumption to speculate on the past distribution of a group by plotting backwards in time the distribution (from Paleobotanical evidence) of certain climatic areas. (Ex. crotalids, Brattstrom, MS.)

The fossil fauna and flora were deposited in the resulting shallow and ephemeral lakes. The climate was subhumid and warm temperate, not unlike the present climate of Monterrey, in the state of Nuevo Leon, Mexico. Warm winters and hot summers prevailed, and abundant sunshine is indicated. The vegetation of the high ground, away from the stream and lake borders, was characterized by pine and evergreen oaks and was probably of an open, scrub-forest type, with grass and microphyll shrubs in the drier areas."

Tortoises living at about the same time and in the same area as the Florissant flora include: *Gopherus laticunea, G. praeextans, Stylemys nebrascensis, Testudo brontops, amphithorax, ligonia, cultrata, quadrata, exornata, thomsoni,* and *peragrans.*[6] Most of these (Williams, 1950a) occur in the Chadron, Oreodon, or Horsetail Creek beds of the White River Formation.

MIOCENE

The Tehachapi flora (Axelrod, 1939), 8 miles west of Tehachapi, Kern County, California includes: *Quercus, Equisetum, Pinus, Cupressus, Typha, Erythea, Sabal, Salix, Populus, Celtis, Ficus, Persea, Umbellaria, Platanus, Cercocarpus, Prunus, Bursera, Rhus, Ceanothus,* and *Fraxinus.* The habitats surrounding the site of deposition, according to Axelrod (1939) were probably: Savanna Woodland, Riperian, Chaparral, Desert Scrub, and Arid Subtropical. This flora is almost in the same geographic area and stratigraphic level as *Gopherus depressus.*

The Mascal flora (Chaney, 1925, 1948) includes: *Sequoia, Ginkgo, Libocedrus, Populus, Salix, Umbellaria, Juglans, Alnus, Quercus, Ulmus, Liquidambar, Platanus, Acer, Ficus,* and *Aesculus.* This is the flora that was dominant over the time and area of the John Day Miocene which includes several species of *Stylemys.*

In one main canyon on the Barstow syncline there is a deposit of fossil fan palms (*Erythea, Sabal,* or *Washingtonia*). The Barstow syncline is the location of *Gopherus mohavense* and *Testudo milleri.*

[6] It should be mentioned here that the relationships and validity of certain of the tortioses listed here and elsewhere is still quite uncertain. Several may be synonyms. This does not detract, however, from their use in the paleoecological discussions.

PLIOCENE

The Ricardo flora (Webber, 1933) includes: *Cupressus, Palmoxylon, Pinus, Quercus,* and *Robinia,* while just some 50 miles to the south, the Anaverde Flora (Axelrod, 1950b) of about the same age, includes: *Pinus,* a palm, *Populus, Salix, Quercus, Persea, Platanus, Amelanchier, Paraphyllum, Eysenhardtia, Dodonaea, Sapindus, Rhus, Ceanothus, Colubrina, Rhamnus, and Bumelia.* The Ricardo formation has yielded fragments of a large, unidentified tortoise.

The Piru Gorge flora (Axelrod, 1950c) of southern California includes: *Equisetum, Sabal, Typha, Populus, Salix, Quercus, Persea, Platanus, Prunus, Rhus, Acer, Fremontia, Ceanothus,* and *Arctostaphylos.* This is stratigraphically just below the beds containing the Hungry Valley tortoise mentioned above.

The Mt. Eden flora (Axelrod, 1937, 1950a) includes: *Equisetum, Pinus, Pseudotsuga, Cupressus, Ephedra, Typha, Populus, Salix, Juglans, Quercus, Ficus, Persea, Platanus, Philadelphus, Cercocarpus, Prunus, Amorpha, Cercidium, Eysenhardtia, Rhus, Dodonaea, Sapindus, Ceanothus, Condalia, Rhamnus, Arbutus, Arctostaphylos, Forestiera, Fraxinus, Chilopsis,* and *Baccharis.* This flora is just a little younger than the deposits in the same area containing the tortoises mentioned by Fick (1921).

The Ogallalla flora from Beaver County, Oklahoma and Logan County, Kansas (Chaney and Elias, 1938), includes: *Celtis, Cercidiphyllum, Cyperacites, Diospyros, Fraxinus, Grymnoclodus, Platanus, Salix, Sapindus, Typha, Ulmus, Acer, Bumelia,* and *Populus.* These beds are just slightly older than the formations which in the same area yielded *Testudo riggsi* and *Testudo rexroadensis* (Oelrich, 1957).

The past distribution of the various groups of fossil tortoises, and the past distribution of certain climates as based on the paleobotanical data are shown in text-fig. 10. It can be seen that the distribution and past ecology of the tortoises conforms with the general picture of changing climates throughout the Cenozoic (*i.e.* a tropical forest spread over most of North America in the Eocene became restricted southward through the course of the Cenozoic to its present posi-

tion; a differentiation of the various vegetation groups or types of temperate and subtropical floras took place in the Oligocene and Miocene; and the present desert came into existence in the post Upper Pliocene. Axelrod, 1949, 1950d, 1952; MacGinitie, 1941, 1953; Chaney, 1940).

ZOOGEOGRAPHY

Other than the fact that most tortoises are tropical in distribution, little can be said concerning the world-wide distribution of tortoises. This is due largely to the lack of knowledge concerning the relationships of the Old World and New World tortoises (Williams, 1950a, 1952). There are some indications, both in fossil and recent species, that certain Asiatic forms are similar, if not identical, with those of North America. (Gilmore, 1931, 1934; Williams, 1950a, 1952; Oelrich, 1957).

The most important feature of the zoogeography of tortoises is that imposed by the paleoecological discussion just presented. For example, relatives of the Central and South American tortoises lacking nuchal scutes, or *Testudo* (*Chelonoidis*), could have crossed the Bering land bridge (or rafted across) only in Eocene or earlier times as this was the only time that tropical or subtropical conditions occurred in this area. In later times these tropical tortoises could probably not have crossed this area as it was not even suitable for them to exist in. Up to Middle Miocene times *Gopherus*, *Stylemys*, and subtropical *Testudo* probably could have crossed (or rafted across) the subtropical and warm temperate Bering land bridge. After Middle Miocene times this area was probably too cool for tortoises.

The evolution of the *Chelonoidis* group of *Testudo* has been described by Williams (1950a) as, "The neotropical tortoises probably differentiated in Central America at a time when this area tended to be separate from both the northern and southern continents (Schuchert, 1935; Weeks, 1948).[7] During this period of differentiation the nuchal scute was lost. Then, probably over a rather narrow sea gap, this progenitor of the neotropical tortoises sent a representative eastward into the West Indies, the ancestor of *T. cubensis*. Southward via Panama another representative went into South America, and southwestward over a much larger sea gap still another to the Galapagos Islands. Isolated in Cuba, perhaps beginning with the Miocene, *T. cubensis* had ample time to develop its special characters." The position of *Testudo* (*Monochelys*) *monensis* is suggested by Williams (1952, p. 558); "Its relationships do not appear to be at all close to any known form, and it may well be a representative of an ancient independent line within the genus *Testudo*, deriving ultimately, no doubt, from a *Hadrianus*-like form." Williams has recently suggested to the writer (personal communication) that, "*Monachelys* may represent an invasion by the Central American stock, *cubensis* by the South American."

The zoogeographic distribution of tortoises requires that rafting or chance, waif, dispersal across water has occurred several times. The dispersal of tortoises to South America, Cuba, and the Galapagos Islands apparently was across water barriers. (Williams, 1950a, 1952, Simpson, 1942, 1943). The most recent geological investigations (Heacock and Worzel, 1955; Shumway, 1953) for example, indicate that there was probably never a land bridge to the volcanic Galapagos Islands. There was, according to these authors, a southward projection from Central America which was probably above water in late Tertiary times. This could afford a possible "stepping-off" point for the Galapagos fauna. The fact that tortoises can cross oceanic areas is evidenced by the observations of Carr (1952, p. 320), "My brother and I once found a giant tortoise swimming off a key in Florida Bay and were no end excited until we learned it was one of C. H. Townsend's specimens introduced on Lignum Vitae Key." And again on page 338 in relation to *Gopherus polyphemus* he mentions, "Gophers are seen with some frequency in the water, but it seems probable that in most such cases they merely fell in. The only individuals I ever saw in water more than shell deep were floating high and flapping their feet pathetically, although they seemed able to maintain a fairly regular course. On two occasions, however, I have

[7] Recent evidence (Durham, *et. al.* 1955) indicates that central America was probably not an island as there apparently was no Isthmus of Tehuantepec seaway.

seen them in the middle of large lakes, fully half a mile from shore."

The distribution of fossil tortoises is plotted on maps (text-fig. 10) along with a summary of the paleoclimatic conditions as evidenced by the paleobotanical data. Certain suggestions concerning the zoogeographic and evolutionary history of tortoises are presented on this map as well.

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JOURNAL OF PALEONTOLOGY, V. 35, NO. 3, P. 561–563, 2 TEXT-FIGS., MAY, 1961

THE BASICRANIAL ARTICULATION OF THE EARLY PERMIAN COTYLOSAUR, *CAPTORHINUS*

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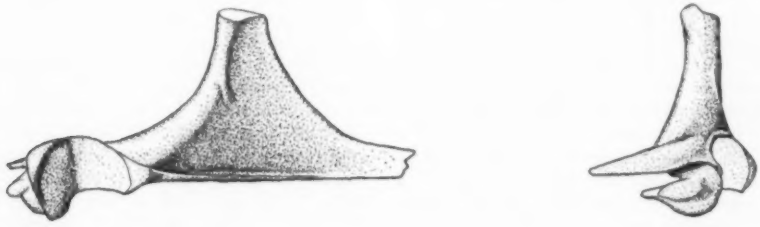
ABSTRACT.—Excellently preserved specimens of *Captorhinus* sp. show the pterygoid to be completely excluded from the cranio-palatal articulation. This is interpreted to be the primitive condition which was modified in later reptiles.

Teeth are described for the first time from the vomer, palatine and parasphenoid bones of *Captorhinus* sp.

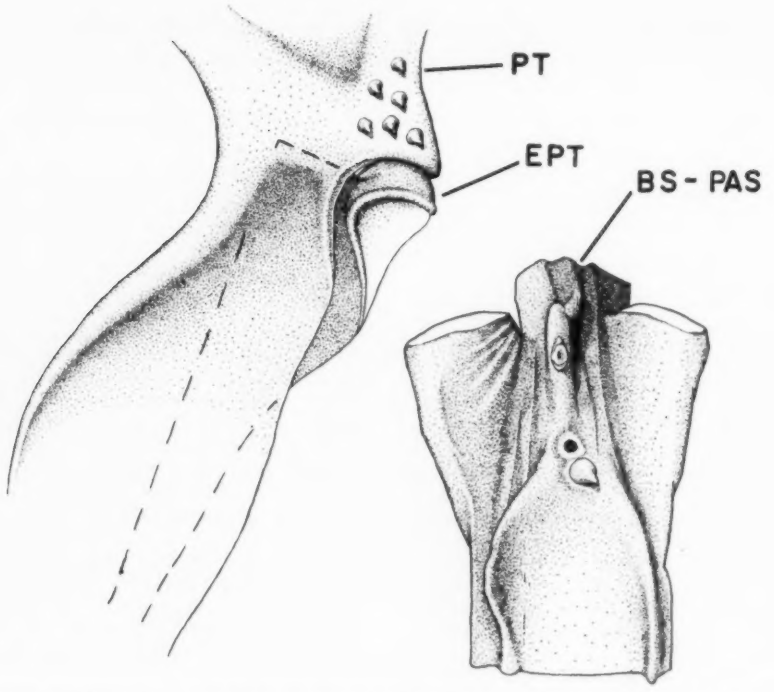
THE nature of the basicranial articulation is not adequately known in any captorhinomorph cotylosaurian reptile. It is best described for Captorhinus (Romer, 1956; Olson, 1951), although even here there remains some uncertainty regarding the incorporation of the epipterygoid into the joint. Detailed information on this joint in Captorhinus would seem to be important in determination of the primitive pattern of the reptilian basicranial articulation. The specimens of *Captorhinus* sp. used in the following description were collected from the lower Permian Fort Sill fissure deposits in Comanche Co., Oklahoma. This paper is in part a direct result of the late F. E. Peabody's investigations into the morphology of Captorhinus and I should like to acknowledge his many suggestions regarding the interpretations of the material.

The epipterygoid (text-fig. 1) possesses a well developed, concave socket at its anteromedial corner for the reception of the basis cranii. Ventral and slightly anterior to this socket there is an anteriorly facing condyle. The lateral margin of the condyle is projected as a small lip to form a groove separating the body of the condyle from an overhanging shelf of the main portion of the epipterygoid. When the epipterygoid is in position on the dorsal surface of the quadrate ramus of the pterygoid, this groove firmly clasps an indented ridge of the pterygoid while the condyle fits neatly into a posteriorly facing fossa. The result of this complicated arrangement is to completely exclude the pterygoid from the basiphenoid-palatal articulation. Text-figure 2 is an illustration of the cranio-palatal joint slightly disarticulated.

I believe that the cranio-palatal articulation exemplified by Captorhinus is primitive. The epipterygoid, ossifying from the palatoquadrate cartilage, was probably originally the sole palatal element involved in the joint. Knowledge of the joint in species of labyrinthodonts which are generally conceded to be close to the phyletic origin of



TEXT-FIG. 1—Right epipterygoid of *Captorhinus* sp. ×6.0. A, median aspect. B, anterior aspect.



TEXT-FIG. 2—Ventral aspect of the basicranio-palatal articulation of *Captorhinus* sp. ×10. Posterior and rostral portions of the basisphenoid-parasphenoid are missing. Reference letters: BS-PAS, basisphenoid-parasphenoid; EPT, epipterygoid; PT, pterygoid.

cotylosaurs is not sufficient to cast any light on the matter. If, as I feel, the epipterygoid-basisphenoid articulation is primitive, then this condition has been lost and the pterygoid incorporated into the joint at least twice in reptilian evolution: once in the sauropsids (using the term to include the reptiles of diapsid affinities), although in some forms a portion of it may remain as the meniscus pterygoideus (Olson, 1951), and again in pelycosaurs. If, as Olson (1951) suggests, Captorhinoides was derived from Captorhinus, then the partial exclusion of the epipterygoid from the joint in Captorhinoides either represents a third independent development of the same situation or serves as evidence to place Captorhinoides (and thus Captorhinus) on the direct line to the pelycosaurs. The latter is not a generally accepted hypothesis for numerous reasons (see Romer, 1945; Olson, 1951).

Watson (1948) feels that the basisphenoid primitively articulated with both the epipterygoid and the pterygoid as it seems to in the pelycosaur, Varanosaurus. He accounts for the exclusion of the pterygoid from the joint in other pelycosaurs by pointing to the relative decrease in size of the brain case and its resultant upward movement so that the basis cranii is pulled away from the pterygoid and onto the epipterygoid. However, Captorhinus, an animal with a relatively large brain case and lacking a deepened temporal region, possesses a laterally directed basis cranii which articulates solely with the epipterygoid, while in lacertilians the problem of a small brain case dorsally removed from the pterygoid has been solved

by a more ventrally directed extension of the basis cranii to reach the pterygoid. I, therefore, suggest that the type of joint found in Varanosaurus is a slight modification from the more primitive condition still maintained by the otherwise more advanced pelycosaurs.

It is interesting to note the occurrence of teeth on more palatal elements in Captorhinus than has been thought. They occur sporadically on the palatine and vomer and are seen on the parasphenoid of the specimen illustrated in text-figure 2. In this specimen there is one entire tooth remaining which is slightly less than 0.5 mm. at its base. Just anterior to this there is the empty socket of another tooth. The broken base of a third tooth is situated at the base of the rostral process on an elevated ridge which serves to place it in the same plane as the other two teeth. Vaughn (1958) discusses the presence of subsphenoidal teeth in other reptiles. It is probably not advisable to place any great phylogenetic significance on slight differences in palatal tooth arrangement owing to the likelihood of cutaneous tooth buds dropping out or migrating from bone to bone (Camp, 1923).

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JOURNAL OF PALEONTOLOGY, V. 35, NO. 3, P. 564–568, 3 TEXT-FIGS., MAY, 1961

STRATIGRAPHIC IMPLICATIONS OF A PERMIAN SPONGE OCCURRENCE IN THE PARK CITY FORMATION OF WESTERN WYOMING[1]

R. M. FINKS,[2] E. L. YOCHELSON[3], AND R. P. SHELDON[3]

ABSTRACT—The lithistid sponge *Actinocoelia maeandrina* Finks has been found recently in abundance in the Franson member of the Park City formation near Dubois, Wyoming. This new occurrence extends the range of the species from west Texas, southern New Mexico, northern Arizona, and southern Nevada to western Wyoming. All previous occurrences are from rocks datable as late Leonard or early Guadalupe (Brushy Canyon). The new occurrence suggests that the Franson member in this area is late Leonard or early Guadalupe age. Stratigraphic and paleontologic evidence indicates that the sponge is essentially confined to deposits made in shallow, clear water of normal marine salinity with an abundant shelly fauna. It is likely that this sponge can be used as an index to the upper Leonard to lowermost Guadalupe interval throughout the Cordilleran area, and as an indicator of a shelf or a shell-bank environment.

INTRODUCTION

NEARLY fifty specimens of the lithistid sponge *Actinocoelia maeandrina* Finks, 1960, recently have been collected from a locality in the Park City formation in the Wind River Mountains near Dubois, Wyoming. The collection is noteworthy for several reasons: it is the only known occurrence of whole sponges in the Park City formation; it is the first recorded occurrence of specifically identified Permian sponges in northwestern United States; it considerably extends the geographic range of a species previously known only from the southwestern United States; it suggests that the Franson member of the Park City formation in this area is an approximate stratigraphic and (or) ecologic equivalent of the Kaibab *beta* of the lower part of the San Andres limestone, of the Victorio Peak gray member of the Bone Spring limestone and of the upper part of the Leonard formation; and it suggests that *Actinocoelia maeandrina* may prove to be a useful horizon-marker and (or) ecologic indicator throughout the Cordilleran region.

THE DUBOIS LOCALITY

This locality was first recorded by Love (1939, p. 34), who presented a faunal list that included two unidentified species of sponges. To the knowledge of the writers, the locality had not been reexamined until Sheldon and Yochelson did so in 1959. Fossils were collected by them along both sides of a fence line in the SW¼, sec. 23, T. 41 N., R. 107 W. (U. S. Geological Survey locality 18605-PC). The locality lies just within the boundary of the Washakie Division of the Shoshone National Forest and is reached by taking a dirt road for 3.5 miles southwest of Dubois, Wyoming, to the spur northwest of Jakey's Fork.

This spur is part of a general dip slope on the east flank of the Wind River Mountains, developed on the upper surface of the resistant cherty limestones of the Park City formation, dipping off the flanks of the mountains. Much of the dip slope is covered with a veneer of Tertiary gravel, but near the upper edge of the dip-slope proper, rock debris characteristic of the Park City formation is scattered over the surface. At an elevation of about 8400 feet the surface begins to slope more gently, cutting across the underlying beds. The sponge locality lies just beyond this crest of the dip surface, and is separated from it by a faint linear swale following the strike of the beds (text-fig. 1). Chips of phosphatic shale float in this depression suggest that it follows the trace of the Retort phosphatic shale member of the Phosphoria formation, that the cherty limestone forming the dip slope is the overlying Ervay carbonate rock member of the

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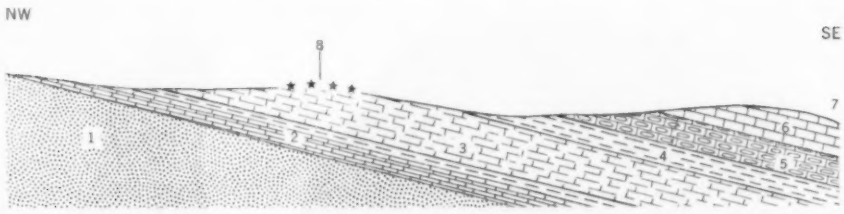

TEXT-FIG. 1—Generalized cross-section at Dubois, Wyoming sponge locality; *1*, Tensleep sandstone *2*, Grandeur member of Park City formation (20 feet) and Meade Peak phosphatic shale member of Phosphoria formation (10 feet) combined; *3*, Franson member of Park City formation (60 feet); *4*, Retort phosphatic shale member of Phosphoria formation (20 feet); *5*, Tosi chert member of Phosphoria formation (40 feet); *6*, Ervay carbonate rock members of Park City formation (40 feet); *7*, Upper edge of dip slope on east side of Wind River Mountains; *8*, fence line. Occurrence of sponges indicated by stars. Horizontal scale about 50 feet to the inch. Stratigraphic thicknesses from unpublished isopach maps prepared by R. P. Sheldon.

Park City formation, and that the sponges come from the top of the underlying Franson member of the Park City. All the collections were made from abundant float only, because no true outcrops are present, but the localized distribution of the sponges and the relatively gentle slope in the vicinity make it likely that the float is essentially in place. The nearest true outcrop, a few hundred feet northwest, is of the Tensleep sandstone, the formation beneath the Park City. Stratigraphic nomenclature of the Phosphoria and Park City formations is given in more detail by McKelvey and others (1959).

The determination of the position of the sponge-bearing beds with respect to the local section has been made on the basis of its position between the Tensleep sandstone and the phosphatic shale. The stratigraphic interval between the nearest outcrops of the Tensleep and the swale containing phosphatic shale float corresponds approximately to the known thickness of the Franson member, as exposed at an excellent section of the Park City on the west flank of Whiterock about 20 miles south of Dubois (see Richmond, 1945), where the Franson is 60 feet thick. About ten feet below the top of the Franson at Whiterock a light gray limestone carries a brachiopod and bryozoan fauna essentially the same as that associated with the sponges. The uppermost beds of the Franson, immediately below the Retort phosphatic shale member, are crowded with *Neospirifer*. At Dubois the *Neospirifer*-bearing beds, are represented by float blocks lying on the slope between the sponges and the phosphatic shale.

Characteristic specimens of *Actinocoelia maeandrina* from the Dubois locality are illustrated as text-figure 2.

DISTRIBUTION AND STRATIGRAPHIC RANGE OF ACTINOCOELIA MAEANDRINA

Actinocoelia maeandrina has been found at localities from west Texas north through the Cordilleran region to western Wyoming (text-fig. 3). The westernmost occurrence is in southern Nevada. All these occurrences appear to be confined stratigraphically to time equivalents of the upper part of the Leonard, and possibly Brushy Canyon, formations of the standard section.

No certain occurrences of this species are known from the standard section of the Permian in the Glass Mountains (1 on text-fig. 3). A related species, however, *?Actinocoelia verrucosa* Finks, 1960, is known from the upper part of the Leonard formation. Restudy of the Leonard collections reveals individuals somewhat intermediate in form between *?A. verrucosa* and *A. maeandrina;* the two species may therefore be more closely related than assumed earlier by Finks (1960).

Twenty-five out of thirty specimens of *A. maeandrina* described by Finks were collected from eight separate places in the Victorio Peak gray member of the Bone Spring limestone in the Sierra Diablo, to the northwest of the Glass Mountains (loc. 2 on text-fig. 3). The Victorio Peak member is

TEXT-FIG. 2—*Actinocoelia maeandrina* Finks from Dubois, Wyoming, U.S.G.S. locality 18605-PC. *A*, exterior, showing characteristic surface texture, U.S.N.M. No. 143219a. ×1; *B*, sagittal section of another specimen, showing the wide radial canals and narrow intervening trabeculae characteristic of this species, U.S.N.M. No. 143219b. ×1.

commonly correlated with the upper part of the Leonard formation, on the basis of both fossil content and stratigraphic position. A few specimens of *A. maeandrina* from the Victorio Peak show some resemblance to *?A. verrucosa* of the Leonard formation, a fact which tends to strengthen the correlation of the Victorio Peak member with the upper part of the Leonard. One specimen of *A. maeandrina* was collected many years ago from Shirttail Canyon in the southern Guadalupe Mountains to the north of the Sierra Diablo (locality 3 on text-fig. 3). It is from dark colored limestone within the Bone Spring formation, but columnar sections shown by King (1948, plate 8) suggest that this locality is correlative with the lower part of the Victorio Peak gray member occurring a few miles to the north. This is the only occurrence of the species known from a basin facies lithology rather than from a light shelf-facies limestone.

The type locality of *Actinocoelia maeandrina* is in the lower part of the San Andres formation transition facies (of Boyd, 1958, page 24) in Last Chance Canyon, central Guadalupe mountains, in southern New Mexico (locality 4 on text-fig. 3). The two most recent studies of the San Andres limestone in this area (Boyd, 1958, p. 63; Hayes, 1959, p. 2212) correlate the lower part of the San Andres, on physical stratigraphic grounds, with the Cutoff shaly member of the Bone Spring limestone or possibly with the uppermost part of the Victorio Peak member beneath the Cutoff. Paleontologic evidence cited by these authors, and observed by the present writers, indicates that the lower part of the San Andres is either uppermost Leonard or lowermost Guadalupe (Brushy Canyon).

The next known occurrences of this species to the northwest are in the Kaibab limestone, *beta* member of McKee (1938, page 13), of the Grand Canyon region in northern Arizona (locality 5 on text-fig. 3). One specimen was illustrated by McKee (1938, pl. 24, fig. a) who reported their widespread occurrence in the *beta* member (facies no. 1) of the Kaibab. Examination of collections of the U. S. Geological Survey, and of the Museum of Northern Arizona, confirms the abundant presence (more than 160 specimens from at least two localities) of *A. maeandrina* in the *beta* member of the Kaibab of the Grand Canyon area. McKee (1938, p. 155) also cites the presence of sponges in the Kaibab limestone of the adjacent parts of Nevada and Utah. Examination of the U. S. Geological Survey collections referred to by McKee shows that *Actinocoelia maeandrina* is present at Goodsprings, Nevada (one specimen), but not in any of the Utah collections cited. McKee

TEXT-FIG. 3—Localities cited in text; *1*, Glass Mountains; *2*, Sierra Diablo; *3*, Southern Guadalupe Mountains; *4*, Central Guadalupe Mountains; *5*, Hermit Trail area, Grand Canyon; *6*, Goodsprings area; *7*, Dubois. *Actinocoelia maeandrina* Finks has been found at localities. 2–7

(1938, p. 171) considers the Kaibab to be the time-equivalent of the upper part of the Leonard formation on both paleontologic and stratigraphic grounds.

No occurrences of this species are known between northern Arizona and the Dubois locality of western Wyoming (locality 7 on text-fig. 3). Because all other known occurrences of the sponge are restricted to beds assignable to upper Leonard or basal Guadalupe age, the Franson member of the Park City formation in this vicinity is here assumed to lie within this stratigraphic interval.

The apparent vertical restriction of *Actinocoelia maeandrina* in the area of the standard section in west Texas cannot be ascribed to lack of collecting, for a rich sponge fauna is known from the immediately underlying and overlying beds (Finks, 1960). Its faunal associates elsewhere indicate a correlation with the same part of the standard section. It would seem, therefore, that the occurrence of this species represents a true time-stratigraphic zone. It is possible that the sponge and some of its associates are facies-controlled, and that the *Actinocoelia maeandrina* zone is time-transgressive. However, since physical stratigraphy tends to confirm paleontological correlations made at each of the presently-known occurrences, an approximate time-equivalence seems likely.

ECOLOGICAL IMPLICATIONS

The occurrence of *Actinocoelia maeandrina* seems to be restricted not only time-stratigraphically but also ecologically. All the occurrences but one are in light, shelly limestones, which give both faunal and physical evidence of deposition in shallow water of normal salinity. The single exception is from the Bone Spring limestone, of basin facies aspect, at Shirttail Canyon, Southern Guadalupe Mountains, referred to in the preceding section; the specimen may have been washed in from the nearby shelf area. Both the Victorio Peak and the transition facies of the San Andres form a narrow zone, interpreted as a shell-bank, between a deeper-water, semistagnant basin on one side and a hypersaline shelf area on the other (King, 1942; Newell and others, 1953; Stehli, 1954; Boyd, 1958).

The sponges at the Dubois locality have overgrown numerous colonies of a branching stenoporoid bryozoan (identified by Helen Duncan, U. S. Geological Survey), shells of the pelecypod *Celtoides*, and the brachiopods *Derbyia* and *Spiriferina*, as well as crinoid stems. The frequency of the incorporation of other organisms into the sponge bodies suggests a rich shelly fauna living on a firm bottom. Some specimens bear shells incorporated on opposite sides of the body, suggesting that they were rolled over by wave agitation in shallow water during their lifetimes. The composition of the associated fauna implies a normal marine environment.

It is likely that the Dubois locality, as well as any locality in which this sponge may occur in abundance, represents a shallow water shelf environment of normal salinity, with little terrigenous sedimentation.

CONCLUSIONS

Because *Actinocoelia maeandrina* is of widespread occurrence in the Cordilleran region in rocks classified as late Leonard or early Guadalupe (Brushy Canyon) on the basis of other evidence, it may indicate a fairly limited stratigraphic zone which will prove useful in correlation. Wherever it occurs in abundance, the sponge probably indicates a clear and shallow water environment of normal marine salinity. Because of its potential usefulness, this easily recognizable sponge should be searched for at localities of probable or possible Middle Permian age.

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JOURNAL OF PALEONTOLOGY V. 35, NO. 3, P. 569–574, MAY, 1961

MAJOR DIVISIONS OF THE CEPHALOPODA

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ABSTRACT—Division of the Cephalopoda into Tetrabranchiata and Dibranchiata involves implications as to the nature of unknown soft parts of fossil forms. Factual and theoretical evidence combine to suggest that many of the features of the Dibranchiata may have developed in their ancestors included in the Nautiloidea, and that many of the features of *Nautilus* are derived, possibly connected with crucial changes in mode of life now known to have occurred in its ancestry.

Use of similar divisions to separate forms with external versus internal shells also involves inferences; recent work has shown this boundary one difficult to draw in relation to primitive belemnites and some supposed bactritids.

It is urged that the tripartite divisions of the Cephalopoda into Nautiloidea, Coleoidea and Ammonoidea is in closer accord with ascertainable facts, and avoids attributing some 3000 extinct genera to a group characterized by the four gills observable only in one genus, the living Nautilus.

CLASSIFICATIONS

LIVING cephalopods are readily divided into two great groups, the Tetrabranchiata and the Dibranchiata. The Tetrabranchiata, represented by only one living genus, *Nautilus*, has an external chambered shell, an eye without a solid lens, four gills, a four-chambered heart, and numerous tentacles. The Dibranchiata have the shells internal or wanting, the eye has a solid lens, there are two gills and a two-chambered heart; tentacles are few, ten or eight in number.

In number of genera and species, the living cephalopods are far outnumbered by the known fossil forms. They are, of course, known almost exclusively from their shells alone. Direct information on the soft parts is limited to perhaps a dozen species known from propitiously preserved specimens, all of which are obviously members of the Dibranchiata. For the vast number of fossil forms assigned to the Tetrabranchiata there is no direct evidence of number of gills or other soft parts. Therefore the suggestion was made that a much more realistic classification would be one in which terms implying knowledge of the number of gills was avoided, and it was proposed that the Cephalopoda should be divided into three equivalent groups, Nautiloidea, Ammonoidea and Coleoidea. Much progress has been made in the understanding of cephalopods since Waagen made this suggestion, but it is still valid, and, indeed, merits of this system have been strengthened rather than weakened by later findings.

Of late several students of the cephalopods have shown a preference for the older dichotomous division of the cephalopods. It is the purpose of the present work to outline the situation, some problems involved, which indicate that the recognition of a tripartite division of the Cephalopoda is preferable as a closer expression of the known morphological facts, and one less involved with assumptions which are not only incapable of proof, but seem to be open to most serious question.

THE COLEOID LINEAGE

It has been accepted for a long time that the first coleoids, the first cephalopods with internal shells, must have developed from orthoconic ancestors within the Nautiloidea. It is now possible to trace the development of the stock with more assurance, and in more detail, back to the oldest and most primitive cephalopods known. The steps in evolution may be summarized as follows:

The archaic cephalopods are those included in the Ellesmeroceratida. Here are endogastric to straight shells, with ventral, primitively marginal siphuncles. Shells are closely septate, most of them are small. The known Cambrian forms are primarily tiny shells, most of them less than a half-inch in length, the largest probably not more than three inches. Close septa suggest that even

if gas was present in the camerae, phragmocones were not buoyant enough to require a vertical position of the shell in life.

With wider spacing of septa and development of a long phragmocone, shells became significantly buoyant. Here various specializations became manifest. Long straight shells, held horizontally in life, were developed, but to maintain the horizontal shell position, the apices had to be weighted in various ways. Three different methods were developed in three great orders, endocones in the Endoceratida, annular deposits in the large siphuncles of the actinoceroids, aided by deposits in the camerae, and cameral deposits in the Michelinoceratida, in which siphuncles were dominatly small and slender. Another line, to be considered more fully in connection with the ancestry of *Nautilus*, was marked by the development of exogastric cyrtoconic shells, with the apex up and the aperture directed obliquely forward and downward in life.

The endoceroids and actinoceroids gave rise to nothing higher; the first group, though prolific in the Canadian, and giving rise to the largest known straight shells in the Ordovician, did not survive the close of that period. The actinoceroids were extremely diverse in the Ordovician, decline after the close of the Silurian, but the group continued in to the late Paleozoic, the youngest forms occur in the basal Pennsylvanian strata.

The Michelinoceratida is a great lineage, as yet not perfectly understood insofar as diverse structures are concerned, and lineages within it can be traced only in broad terms. It is, however, evident that it gave rise to two groups with quite similar phragmocones, the bactritids and the first belemnoids. Both have presumably, apices in which the swollen protoconch was recognizable. This development, however, is a relatively ancient one; such protoconchs have been found in generalized Michelinoceratida as far back as the late Trenton (Ruedemann, 1912). Phragmocones agree further in a ventral siphuncle and a tendency for development of a compressed cross section; sutures may be straight or faintly sinuate. Phragmocones of this type are common to the bactritids and the belemnoids, and without other features, such phragmocones cannot be assigned with certainty to one group to the exclusion of the other (Flower and Gordon, 1959). True bactritids, as known from the Devonian, have all the features of external shells. Some are very thin shells, which might have been internal, but some others are thick, and show growth lines quite like those of straight nautiloids in which there has never been reason to question the external position of the shell. A good many Devonian forms are known to possess long slender living chambers.

The oldest known belemnites, those of the Mississippian, develop rostra of appreciable size. Within, the phragmocones show the general pattern of bactritid or supposed bactritid shells. Some forms, notably *Bactritimimus*, are known mainly from bits of phragmocone. Indeed, only fragments of rostrum on one of the five specimens representing the genus *Bactritimimus* show that the rostrum was present, and that the shell was internal. Without this specimen, the phragmocones would certainly have been placed in the family Parabactritidae.

Not much is known of the anterior ends of the oldest belemnoids. *Eobelemnites* shows by its growth lines that the anterior end was probably extended into a long proostracum on the dorsum, with a shorter one on the ventral side. For other genera even this bit of evidence is wanting. It is, however, evident that the conotheca extended as a wall, continuous around its circumference, some distance anterior to the last septum. How far it extended is not known; all specimens so far found are broken anteriorly. It is, however, evident that these older belemnoid phragmocones agree in general features with shells constituting the family Parabactritidae. Such shells were regarded as external, and as a group of the bactritids. Living chambers are cited as evidence of the external nature of the shells. To this, two objections can be raised: (1) the figured specimens show as "living chambers" only aseptate forward extensions of a conotheca not materially longer than those seen in the belemnoid *Bactritimimus*. (2) Is an anterior aseptate conical part of a shell which could be called a living chamber certain evidence

that the shell was external? The assumption that it necessarily constitutes such evidence is questionable.

Certainly the presence of a rostrum is clear evidence of the internal nature of a straight chambered shell. Absence, or apparent absence, of a rostrum is inconclusive. It has been assumed that as soon as the mantle grew over the ancestral "orthoceran" shell it began to secrete a rostrum, and that the tubular long living chamber was reduced to a proostracum, but we have no assurance that these two distinct developments did not follow enclosure of the shell by the mantle, possibly there might have been a considerable delay in time involved. Tubular anterior empty bits of shell which could be called living chambers have been attributed to Triassic belemnites from time to time; today it seem that most, if not all, such instances result from misidentification of living chambers of associated Michelinoceratidae with the belemnites, but the possibility that such anterior conical aseptate bits of shell were retained in the older belemnites is one not to be dismissed too readily. Present evidence seems to suggest that the entire Parabactritidae might be based upon belemnite rather than bactritid phragmocones, but the rostrum was exfoliated from all known specimens.

It is sufficient, without exploring further perplexities of the problem of distinguishing the early belemnitids from real and suspect bactritids, to note a strong general similarity of phragmocones, suggestive of a very close relationship; further, this relaionship is continued into certain forms in the Michelinoceratida, two genera, one as yet unpublished, including *Orthoceras winchelli*, Meek and Worthen, the other the genus *Arkonoceras*, approach rather closely to the common pattern shown by the oldest belemnites and the bactritids. In digression, it may be noted that while the origin of the bactritids in the Michelinoceratida seems to be beyond dispute, the position of these shells as primitive ammonoids remains highly questionable, though the thesis is still not without its proponents. However, present evidence indicates that similar as are the bactritids and simpler Ammonoidea in internal organization, there remains a wide gap in shell form, for cyrtoconic bactritids are not known, and the most loosely coiled ammonoids are gyrocones. Elsewhere, (Flower, 1955) I have shown reasons why the transition from a cyrtocone to a gyrocone was saltational, but acceptance of this wider gap in form types seems highly suspicious, and indicative of homeomorphy rather than a real realtionship.*

Difficulty in distinguishing the first belemnoids from associated types with external shells is significant in two ways. (1) It shows the real relationship of the first belemnites with forms with external shells which should properly be included in the Michelinoceratida. Further, the transition was a simple one, not involving any great change in the mode of life. Michelinoceratida were dominantly nektonic organisms, and the shell, with its apex weighed by cameral deposits, was held horizontally in life. (2) The first belemnoids lived in much the same way, but the rostrum became the main factor in hydrostatic adjustment. Cameral deposits are still retained, but they are thin, and plainly merely vestiges retained as a no longer needed inheritance.

THE *NAUTILUS* LINEAGE

It is now evident that *Nautilus* is the last of a long line of coiled shells which we can trace back with some certainty to *Centroceras* and the Centroceratidae in the Middle Devonian. The ancestry of *Centroceras* is less clearly indicated by adult or ontogenetic similarities, but there is hardly any other possible ancestor than the earlier Devonian members of the Rutoceratidae. Origin of the Rutoceratidae was for long a problem, because ancestry was sought in older coiled

* Since this was written, an apparent contradiction of the above statement has come into my hand, a significant contribution by H. K. Erben (Primitive Ammonoidea aus dem Unterdevon Frankreichs und Deutschlands, Neues Jahrb. Geol., Paläont., Abh., vol. 110, p. 1–128, 6 pls.) in which is described the genus *Cyrtobactrites*. This genus contains curved shells, extremely slender. One specimen describes a half volution, and there is no certainty that it is complete. I regard *Cyrtobactrites* as a gyroconic shell, allied to *Kokenia*. A wide gap in form separates both of these genera from the perfectly straight Bactritidae *Bactrites*, *Lobobactrites* and *Pseudobactrites*.

shells, and none were known which showed the proper morphological features. Instead, it was found that the expanded siphuncles and actinosiphonate deposits found in some of the older Rutoceratidae pointed to an ancestry where it was least suspected, in the group of cyrtochoanitic cyrtocones of the Ordovician, the Oncoceratida. This order is further traceable back to the Basslerocera-tidae, of the Canadian, the first truly exogastric cyrtocones, and that family finds its origin in the archaic Ellesmeroceratida. In tracing this progression forward, it is evident that there are two points at which marked changes in shell form and, from all analogy, in mode of life occurred. The first is the development of the exogastric cyrtocone, in which the apex of the shell was pointed upward, and the aperture faced obliquely down and forward. The second is the development of a shell of more than one volution, and here the aperture was essentially vertical, facing directly forward.

SOFT PARTS

The inclusion of fossil cephalopods (Nautiloidea and Ammonoidea) with external shells in the Tetrabranchiata, and even the inclusion of a respectable group of such forms in the Nautiloidea, results every now and then in the temptation to attribute to either or both of these categories the features of the soft parts known from *Nautilus*. Thus one encounters every now and then assertions that all of the "Tetrabranchiata" had the many short tentacles of *Nautilus*, the simple eye, the four gills and other anatomical similarities. Yet theoretical considerations should lead us to view these conclusions with suspicion. It is, after all, in connection with changes of the mode of life that profound anatomical changes are correlated; we find them strikingly displayed, furthermore, in the parts of the animal which come into closest contact with the environment. Striking and familiar examples are the changes in the feet and teeth of the Mammalia, but connected with the grazing habit of the ruminants are some bizarre specializations of the digestive tract. If we are to review the evolution of the cephalopods and postulate similar points, marking changes in the mode of life as places where one may expect to find great potential modifications of structure of the main body of the animal, where will they be located? In the ancestry of the Coleoidea one finds the primitive endogastric cyrtocones giving rise to straight shells, held horizontally in life in stocks which were dominantly at least quite motile, if not altogether nektonic. No profound change in mode of life marks the inception of the first Coleoidea. It seems then quite reasonable to believe that the ancestors of the Coleoidea might well have possessed many of the features of that group, even though, because they have external shells, they have been called Tetrabranchiata and Nautiloidea, and from the application of these terms the reverse has been widely assumed. In the ancestry of *Nautilus*, however, there have been two points, the development of the exogastric cyrtocone (first apparent in the initiation of the Basslero-ceratidae in the Middle Canadian) and then of the first coiled shells (the first Rutocerati-dae, in the lowest Devonian) mark two changes in the mode of life. With either or both of these, there is a great potential for specializations in the soft parts.

Some propitiously preserved specimens of belemnites and other fossil Coleoidea show, to varying extents, an organization agreeing with that of living forms, a relatively small number of arms, development of an ink sac. Such evidence as is afforded by these specimens indicates a general accord of body organization with that of living representatives. It is not too much to hope that these features were shared by archaic members of the group, and even their ancestors in the Michelinoceratida. Until quite recently there has been no indication of the structure of any of the soft parts of any of the cephalopods with external shells. Recently the writer (Flower, 1955a) described trails and tentacular impressions attributed to straight cephalopods in the Cincinnatian. They suggest a motile mode of life, not unlike that of living Coleoidea, and markings interpreted as tentacle impressions indicate that there were relatively few arms as in the squids, not many short arms as in *Nautilus*. If these impressions are correctly interpreted, and no better explanation has been proffered, they support the suggestion that tentacle arrangement of the coleoids goes far back in the nautiloid ancentry of the stock.

Reasons for regarding *Nautilus* as specialized in accordance with changes in mode of life, suggest that the coleoid pattern might be more primitive than had been generally supposed. At the time when the trails were described they were attributed to *Orthonybyoceras*, the dominant orthoconic cephalopod of the Cincinnatian. The generic assignment seems beyond reasonable doubt, but there is some uncertainty as to the position of the genus. It has previously been regarded as an actinoceroid. If this is true, it is not in the direct ancestry of the coleoids, but an independent line, and to connect it with the coleoids the ancestry of the genus must be traced back through the more primitive actinoceroids into the Ellesmeroceratida, and thence forward through the Michelinoceratida. This attribution may be questioned from recent evidence which, though incomplete, suggests that *Orthonybyoceras* may not be an actinoceroid, but instead a development within the Stereoplasmoceratidae, a family of the Michelinoceratida characterized by an expanded siphuncle and rather singular siphonal deposits. This family was differentiated by Chazyan time, and extends up through the higher Ordovician, and its last known descendant, the rather aberrant genus *Cyrtactinoceras*, is of late Middle Silurian age. Thus while the general coleoid pattern of tentacle arrangement is not necessarily archaic in regard to the cephalopods, it is at least one fundamental to the Michelinoceratida from a point close to the inception of that order.*

There is still no evidence as to the tentacle number in the archaic ellesmeroceroids and their short-lived descendants comprising the orders Discosorida, Endoceratida, and Actinoceratida, but the form changes in the ancestry of *Nautilus* leave it somewhat simpler to believe that these orders had tentacles of the coleoid pattern rather than of the type found in *Nautilus*.

There is, then, reason to believe that the tentacle pattern of the coleoids was developed in the ancestral Michelinoceratida, and that it might reasonably have been a feature of primitive nautiloids in general. It makes even more precarious than before the assumption that gills and other soft parts of the extinct cephalopods with external shells necessarily duplicate those of *Nautilus*. The implications involved in the inclusion of these forms in the "Tetrabranchiata" then appears even more misleading than it did before.

* Recent work shows the first of the Michelinoceratidae, not previously known with certainty prior to the pre-Chazyan and post-Canadian Whiterock intervals, in beds of latest Canadian age. The forms involve the first of the true Michelinoceratidae, and the first of the Troedssonellidae. Details will be presented on another occasion.

EXTERNAL VERSUS INTERNAL SHELLS

It has been suggested that Dibranchiata and Tetrabranchiata are convenient terms, because of their long familiarity, for cephalopods separated on the basis not of gill number necessarily, but of those with external versus internal shells.

In doing so, we are merely replacing one inference for another. It is, to be sure, a logical inference, but suggestions have been made from time to time, to the contrary. Prell (1921) suggested that the visored brevicones, which he treated as *Phragmoceras* in the broad sense, had internal shells. The suggestion has been made that Ammonoidea might be Dibranchiata. Today, neither suggestion seems convincing, but opposing evidence is supposition rather than fact. Difficulties in distinguishing from fragmentary remains, with which we are oblighed to deal, the primitive belemnites and the bactritids in the Mississippian offers another facet to the perlexing aspects of the problem. The separation of external from internal shells is not a simple matter, and the problems involved are perplexing enough to leave it a somewhat embrarrassing point to draw a line between major categories.

One may also suggest that, if such a division is to be accepted for the Cephalopoda, why would it not be an equally appropriate division in other molluscs. We could, by this means, evolve major groups of the Pelecypoda including most forms in one group and *Teredo* and its allies in the other. We could divide the gastropods in the same way. Probably nothing of the sort has been suggested because in both Gastropoda and Pelecypoda the forms which have shells internal or wanting are relatively small groups.

SUMMARY

Divisions of the Cephalopoda into Nautiloidea, Ammonoidea and Coleoidea produces a system which, in relation to the Tetrabranchiata and Dibranchiata, is relatively factual. True, there remain perplexities, but they are lessened, and major categories are less dependant upon inferences which seem highly questionable. A problem still exists as to whether some straight shells were external or internal, whether perhaps internal shells developed some time before the initiation of the rostrum. Here this point may be avoided, regarding the Coleoidea as beginning only with the inception of the secretion of the rostrum, which, as a new addition to the shell pattern, supplies a more convenient point of demarcation than speculations as to the internal or external nature of the shells. Perhaps our suppositions on these matters are far from the facts. Without living forms, would it have been clear that the shells of *Cypraea* and its allies were covered by a mantle in life? Except for differences of opinion as to the role of the Bactritids, there seems to be little confusion as to the limits of the Ammonoidea, though it seems that the independent origin of the clymeniids remains a possibility not yet fully investigated. With these reservations, there seems little difficulty in recognizing the scope of the Ammonoidea.

With recognition of three major divisions of the cephalopods, one great vexation is removed. We are no longer employing the Tetrabranchiata in which the number of gills known from the one living genus is attributed by wishful thinking to the more than 3000 extinct genera. Surely it is time that paleontological works abandon a classification of the cephalopods on the basis of the number of gills which we hope they had.

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JOURNAL OF PALEONTOLOGY, V. 35, NO. 3, P. 575–577, 1 TEXT-FIG., MAY, 1961

A NEW SPECIES OF HADROSAURIAN DINOSAUR FROM THE CRETACEOUS OF NEW MEXICO

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ABSTRACT—A new species of *Parasaurolophus*, *P. cyrtocristatus*, is recorded from the Fruitland formation of the San Juan basin, New Mexico.

INTRODUCTION

DURING a recent investigation by the present author of the cranial morphology of North American hadrosaurs, Dr. Rainer Zangerl, of the Chicago Natural History Museum, called the author's attention to a nearly complete skeleton of *Parasaurolophus* in the collections of that institution. Originally discovered and collected by Mr. C. H. Sternberg in 1923 from the Fruitland formation of northwestern New Mexico, this specimen had only recently been prepared and no formal announcement of its discovery had been published. This is the first known crested hadrosaur to be recovered from the Fruitland, although fragmentary hadrosaurian remains have been known from this formation for many years.

Comparison of this specimen with the other species of *Parasaurolophus* (*P. walkeri* from the Belly River of Alberta and *P. tubicen* from the Ojo Alamo of New Mexico) demonstrates that it represents a new hadrosaurian species. The present paper is presented as a preliminary announcement of this new species. A more detailed study of this specimen is planned for future publication.

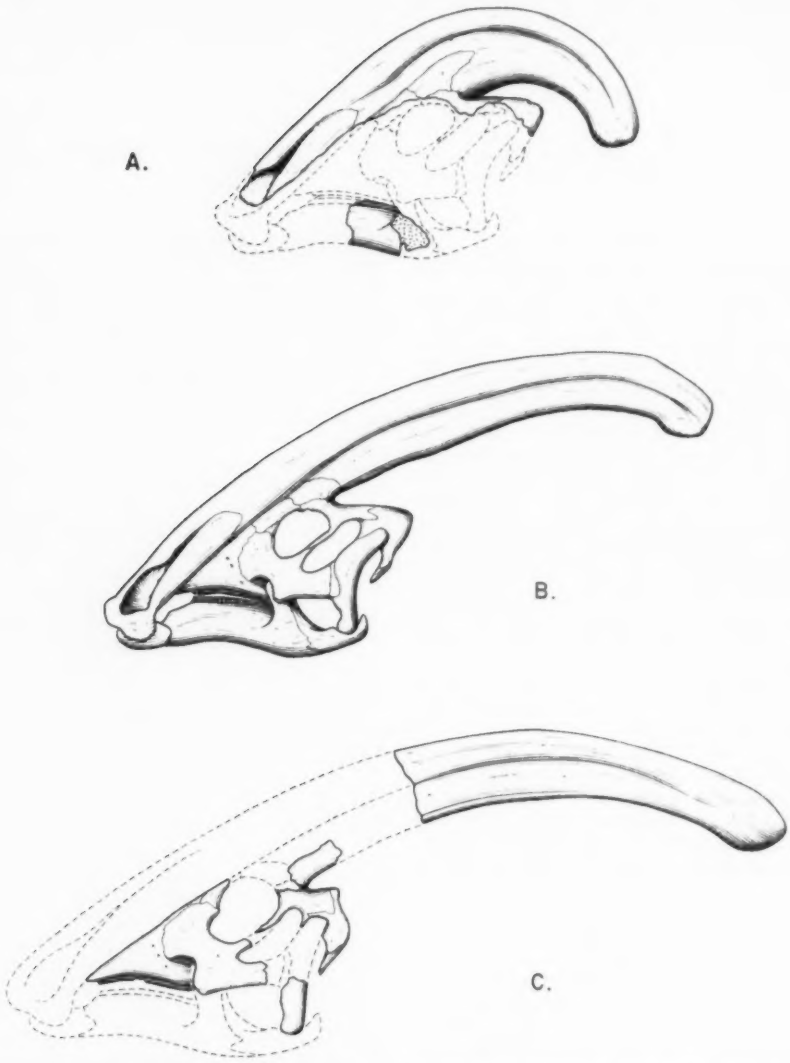
SYSTEMATIC DESCRIPTION

Class REPTILIA
Order ORNITHISCHIA
Suborder ORNITHOPODA
Family HADROSAURIDAE Cope, 1869
Subfamily LAMBEOSAURINAE Parks, 1923
Genus PARASAUROLOPHUS Parks, 1922
PARASAUROLOPHUS CYRTOCRISTATUS
Ostrom, n. sp.
Text-fig. 1a

Holotype.—Chicago Natural History Museum, No. P27393; complete cranial crest and dorso-caudal part of the cranium, fragmentary left dentary, 3 cervical vertebrae, 11 dorsal vertebrae, 8 sacral vertebrae, 26 caudal vertebrae, both scapulae and humeri, right radius, fragmentary left radius, right ulna, fragmentary left ulna, both ischia, ilia, pubes, femora, and tibiae, left fibula, incomplete right fibula, and numerous ribs, chevrons and phalangeal elements.

Occurrence.—Fruitland formation (Maestrichtian?) near Coal Creek, eight miles southeast of Tsaya, McKinley County, New Mexico. (This locality is not to be confused with a "Coal Creek" ten miles north of Tsaya in San Juan County.)

Diagnosis.—Cranial crest approximately one third as long as that of *P. walkeri*, extending only 260 mm. behind the occipital crest (as compared with approximately 860 mm. in *P. walkeri*). The crest curves strongly downward behind the occiput, rather than extending dorso-caudally in a gentle arc as in *P. walkeri* and *P. tubicen*. Total length of the superior skull margin from the rostral end of the premaxilla to the posterior extremity of the crest exceeds 1425 mm. (the anterior extremities of the premaxillae are missing), as compared with 1733 mm. in *P. walkeri*. As in other species of *Parasaurolophus*, the cranial crest is composed almost entirely of the premaxillae. The nasals appear to be very small elements restricted to the posterior basal portion of the crest. The paired narial passages, separated by a median bony septum, extend over the total crest length, looping back beneath themselves in the ventral posterior part of the crest and passing forward to a common orifice in the interorbital region. This pattern closely resembles that of *P. walkeri*, but is distinct from that of *P. tubicen* in which the median septum is lacking. Except for



TEXT-FIG. 1—Comparison of the skulls and crests of the three species of *Parasaurolophus*. A, *P. cyrtocristatus* (Chicago Natural History Museum No. P27393), approximately 1/16 natural size. B, *P. walkeri* (Royal Ontario Museum No. 768), approximately 1/16 natural size. C, *P. tubicen* (University of Upsala, Sweden), approximately 1/16 natural size.

fragments of the frontals, parietals and exoccipitals, the remainder of the skull of *P. cyrtocristatus* is unknown.

Remarks.—The distinctive form (strong ventral deflection) and small size of the cranial crest are the only diagnostic features displayed in this specimen. This conforms with the general situation in the Hadrosauridae where nearly every species is distinguished solely by cranial characteristics. With one or two exceptions, there are no reliable generic or specific characters of diagnostic significance in the hadrosaurian post-cranial axial or appendicular skeleton. The numerous hadrosaurian species display conspicuous uniformity in their post-cranial morphology, but show a remarkable degree of variation in their cranial anatomy. This is particularly true of the crested species assigned to the Lambeosaurinae.

Although the greatest part of the skull of *P. cyrtocristatus* is unknown, the premaxilla length indicates a skull size somewhat larger than that of *P. walkeri* and perhaps as large as that of *P. tubicen*. Therefore, the shorter post-occipital crest length cannot be interpreted as an immature or juvenile condition. This is substantiated by the limb dimensions of this specimen, which exceed those of *P. walkeri* by approximately 10 to 20 per cent. The short crest length is therefore considered to be of phylogenetic significance rather than ontogenetic variation.

In most respects, the post-cranial skeleton is very similar to that of *P. walkeri* (the skeleton of *P. tubicen* is not known). The humerus–radius ratio, however, conforms to the typical lambeosaurian condition, with the radius length (585 mm.) exceeding the length of the humerus (565 mm.), in contrast to the exceptional condition found in *P. walkeri* where the humerus (520 mm.) is longer than the radius (496 mm.). The ischia are expanded distally, as they are in all species of the Lambeosaurinae.

ACKNOWLEDGMENTS

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JOURNAL OF PALEONTOLOGY, V. 35, NO. 3, P. 578–579, 1 TEXT-FIG., MAY, 1961

A LATE CRETACEOUS MAMMAL FROM DRAGON CANYON, UTAH

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ABSTRACT—An upper molar of *Pediomys hatcheri* (Osborn), probably derived from the "Cretaceous portion" of the North Horn formation, was discovered in Dragon Canyon, Utah.

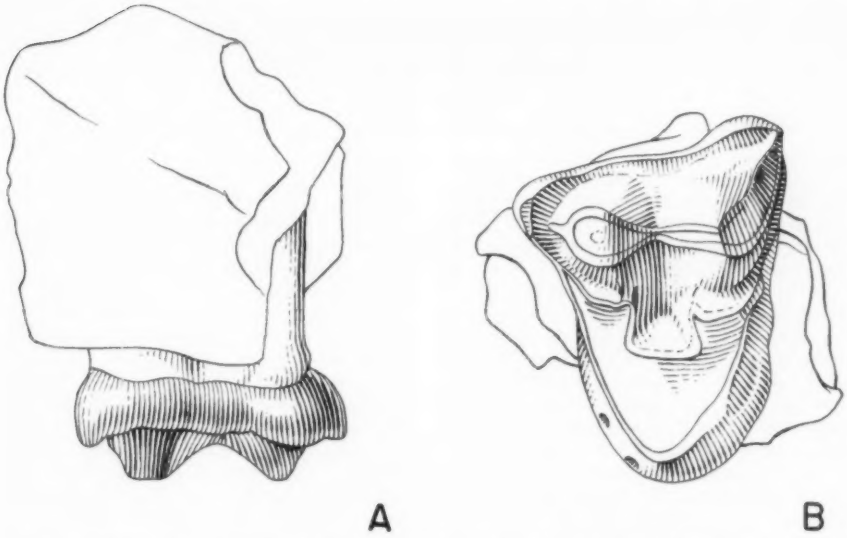
IN 1958 the tooth of a Cretaceous mammal was found in Dragon Canyon on the eastern side of the Wasatch Plateau by a field party working under the direction of Dr. Malcolm C. McKenna. This discovery is of particular interest for it greatly enlarges the demonstrated zoogeographic range of North American, Late Cretaceous mammals. Because I was engaged in research on a new collection of Cretaceous mammals from the Lance formation of eastern Wyoming, Dr. McKenna kindly turned over the specimen to me for study. I am indebted to Drs. D. E. Savage and R. A. Stirton who have constructively criticized the manuscript. The illustrations are the work of Mr. Owen Poe.

The fossil (Univ. Calif. Mus. Paleontology no. 55640, text-fig. 1) is a therian upper molar preserved in a fragment of maxilla. The protocone of the molar is heavily worn; its wear-facet is confluent with those of the protoconule and metaconule. The protoconule and the anterior stylar cusp are connected by a narrow cingulum. Although worn, the paracone and metacone appear to have been of approximately equal size. The stylar shelf is continuous across the labial side of the paracone. On the ridge along the labial edge of the shelf there is a small, elongate stylar cusp opposite the metacone. The coronal dimensions of the molar are as follows: length = 3.65 mm., width = 5.00 mm. In size and morphology the tooth is indistinguishable from typotypic M^3's of *Pediomys hatcheri* (Osborn) collected from the Lance formation in eastern Wyoming. The similarities may not prove to be diagnostic of the species or even the genus, but at present there are no controverting data.

The mammal tooth was found on an anthill near the United States National Museum quarry where the type of *Polyglyphanodon sternbergi* Gilmore, a large lizard, was recovered. This locality is in lower Dragon Canyon; S ½ sec. 17, T. 19 S., R. 6 E., Emery County, Utah [see Gazin (1941) for additional locality data and a study of the geology of the area]. The strata exposed in and adjacent to the quarry have been referred to the "Cretaceous portion" of the North Horn formation. The basis for this age determination has been summarized by Spieker (1946). Strata referred to the "Paleocene portion" of the formation crop out several hundred feet east of the locality. Experiments have shown that ants can transport small fossils across distances approximating 100 feet, but the disposition of the anthill suggests that the molar was probably derived from the "Cretaceous portion" of the formation.

Prior to 1958 almost all North American, Late Cretaceous mammals had been found at sites east of the Rocky Mountains in Alberta, Montana, Wyoming, and South Dakota. The only specimen reported from a locality within the mountain system is a mammal tooth found near Red Lodge, Montana (Jepsen, 1931). The *Pediomys*, molar from Dragon Canyon is the second specimen to be found within the Rocky Mountain province and extends the zoogeographic range of Late Cretaceous mammals far to the south of their previously demonstrated North American distribution.

Pediomys hatcheri is a common mammal in the fauna of the Lance formation of eastern Wyoming. It has not been reported from other, northern localities, but its absence could be attributed to the lack of adequate samples from these sites. *Pediomys hatcheri* has not been found in Tertiary deposits, and apparently it was not ancestral to any



TEXT-FIG. *1*—Left upper molar of *Pediomys hatcheri* (Osborn), Univ. Calif. Mus. Paleontology no. 55640. A, labial view, ×8. B, occlusal view, ×8.

of the presently known Tertiary mammals. Probably the biozone of the species is restricted to the North American Upper Cretaceous, but its limits still are not adequately determined. Therefore, the occurrence of *Pediomys hatcheri* in the "Cretaceous portion" of the North Horn formation is in accord with but cannot be used at present for a further refinement of the Late Cretaceous age assigned to this part of the formation.

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RECENT LITERATURE ON MESOZOIC AMMONITES, CONTINUED

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EVER since the conclusion of my earlier essay-review on the same subject (Haas, 1958), the steady flow of publications dealing with Mesozoic ammonites has continued at such a rate as to justify the present attempt to review this new output before the task becomes unmanageable. By May 1960, more than 100 papers have accumulated that were not included in my earlier review. Among them were several that were published before conclusion of my review but for various reasons not covered by it.

By my count, which is certainly not complete, althogether 50 new generic and subgeneric names for Mesozoic ammonites which are not found in volume L of the Treatise on Invertebrate Paleontology have been proposed in those papers. Nearly all these names have been published after 1954 and all of them must be added to the 72 valid plus 39 suppressed generic names published during the period 1758–1954 which are listed by Howarth (1960) and which are not included in the Treatise either.

For this continuation completeness cannot be claimed any more than it could for my first review, and the reservation then made as to selectiveness holds true for this one, too. Of papers published in 1960, only a few that appeared early in that year are included.

It is proposed to discuss first ammonite studies of a more general interest, then those dealing with Triassic, Jurassic, and Cretaceous Ammonoidea, in that order.

I

In 1958 I reviewed volume L of the Treatise on Invertebrate Paleontology. Since then, its Russian counterpart (Luppov & Druschitz, 1958) has come out. Having been reviewed only recently quite extensively in this Journal (Connors and Yochelsen, 1960), it can be omitted in the present review.

In another paper, of a more general scope Beurlen (1957) speculates profusely on the functional significance of aberrant shell shapes in ammonites. Although conceding the occurrence of a few aberrant forms in the Upper Triassic and in the middle Jurassic, the author begins with the assumption that the "Ammonoidea stick rigidly to a normal, closed, planispiral" shell shape "from the Devonian to the Cretaceous." However, this assumption seems to be inconsistent with the fact that such aberrant forms occur commonly throughout the Mesozoic. *Choristoceras*, *Peripleurites*, *Rhabdoceras*, and *Cochloceras* appear in the late Triassic, *Arcuceras* in the Lower Jurassic (Pliensbachian), *Spiroceras* and *Apsorroceras* in the middle Jurassic (Bajocian), *Parapatoceras* somewhat later (Bathonian-Oxfordian). Furthermore, we encounter many (at least 45) genera of the Bochianitidae, Ancyloceratidae, Heteroceratidae, Hemihoplitidae, and Ptychoceratidae in the late Jurassic and early Cretaceous, and those of the Hamitidae, some Baculitidae, and all the genera of the Anisoceratidae, Turrilitidae, and Labeceratidae in the middle Cretaceous (Aptian to Turonian). A few baculitid genera extend into the Senonian, and only the families of the Phlycticrioceratidae, Nostoceratidae, Diplomoceratidae, and Scaphitidae can be considered essentially Upper Cretaceous in age. Among the genera of thsee four families only *Nostoceras*, *Axonoceras*, *Exiteloceras*, *Solenoceras*, *Neocrioceras*, *Cirroceras*, *Emperoceras*, *Neancyloceras*, *Diplomoceras*, *Pravitoceras*, *Phylloptychoceras*, *Ryugasella*, *Rhaeboceras*, *Hoploscaphites*, *Indoscaphites*, and *Acanthoscaphites* do not appear until the Campanian and can thus be assigned a late Cretaceous age. By this enumeration it is meant to show that the aberrant ammonites of the late Triassic and the Dogger are by no means negligible, that hosts of such forms emerge throughout the Mesozoic and that aberrant ammonites are therefore not at all a peculiarity of the late Cretaceous. (It may

be well to remember at this juncture that similarly aberrant Nautiloidea, such as *Goldringia*, in the shape of an open spiral, and *Lorieroceras*, resembling a sinistral gastropod, appear in the Devonian). It is for the above reason but not for those suggested by Beurlen, to be mentioned presently, that most ammonite workers today reject the interpretation of the aberrant forms as effects of racial senescence.

In the introductory paragraphs of his paper Beurlen admits that the shell shapes of these aberrant forms defy "at first" a plausible biological explanation. I fully subscribe to this this, except for the qualification "at first." The author, however, rather than resigning himself to the realization that we are facing here the free play of evolution as it creates all possible forms (even most improbable ones such as *Nipponites*), play that may in some cases be interpreted as adaptive radiation, speculates further about what mode of life—nektonic, planktonic, etc.—could be indicated by those manifold shell shapes. In this procedure, he cannot well escape the danger of overgeneralization. The main example of this is his repeated assertion that the aberrant forms represent the "last" cycle of ammonitic evolution, an opinion amply refuted by the above enumeration. He also believes in a trend toward an increasing degree of involution; however, evolute forms occur among late ammonites (e.g., *Peroniceras*, *Texanites*) as well as among early ones. Beurlen also considers strong ornamentation a late character, unaware of the fact that a considerable number of late, and even latest ammonite genera (*Placenticeras*, *Sphenodiscus*) are nearly or perfectly smooth. Similarly inconsistent with the facts is the author's assumption that the length of the body chamber decreases in the course of ammonite evolution; for the shortest body chamber ever recorded (1/20 of a whorl) was found in the Maestrichtian genus *Sphenodiscus*. Some of his arguments are based on the hypothesis that the soft body of later ammonites projected—permanently, as his article seems to indicate—from the shell and embraced increasingly larger portions of it, but this hypothesis will be accepted by few, if any, students of ammonoids (see also below, Géczy, 1957). The author also claims for ammonite aptychi some other function than that of an operculum serving to close the shell; this claim is certainly refuted by Schindewolf, 1958 (see below). And so the problem continues. There is hardly a trend mentioned against which an opposite one cannot be quoted, and examples repeatedly come to mind that may be relied upon to prove the opposite of what the author infers from his chosen examples. This applies mostly to Beurlen's main thesis which attempts to explain all the manifold aberrant shell shapes as means to a better adaptation toward a free swimming way of life. Here I cannot suppress the question: What about *Nipponites?* Summarizing, I conclude that Beurlen's argumentation is insufficiently documented and unconvincing.

Schindewolf (1957) defends his method of careful study of the earliest ontogeny of ammonoid sutures against Arkell's refutation of Westermann's septal hypothesis (see Haas, 1958, p. 627). In a study of Mississippian juvenile cephalopods the same author (1959) finds the constancy and phylogenetic significance of early sutural stages, as advocated in the paper just mentioned, further confirmed. Schindewolf's monograph on aptychi (1958), triggered by the discovery of a magnificently preserved specimen of the late Jurassic *Physodoceras* cf. *altenense* (d'Orbigny) with the aptychi *in situ*, must certainly be considered a contribution of lasting importance. In opposition to Trauth, generally considered the greatest authority on aptychi, a dorsal rather than ventral position in the aperture, corresponding to the site of the hood in *Nautilus*, is here postulated for them. The different, so-called normal position of aptychi frequently found in fossils, for example in all 14 juveniles of an oppeliid species accumulated on a single slab of limestone from Eichstätt, Bavaria, seen in plate 7 of this paper, is believed to be caused by the mode of decomposition of the soft parts. The microstructure of various kinds of aptychi is carefully studied and clearly illustrated.

In addition to several descriptive papers on both Jurassic and Cretaceous ammonites, to be covered later in this review, Reyment published in the last few years also three of a more general interest. The most important of these (1958d) seems to be a careful study,

largely based on experiments with empty *Nautilus* shells, of factors influencing the distribution of fossil cephalopods. The results arrived at in this investigation are much too numerous to be summarized here. It should be noted, however, that in the author's opinion the oceanic barriers impeding the spread of living shelled cephalopods need not have hindered the floating of their empty shells and that a much wider geographic range could thus have been attained by the latter than by the former. Occasionally empty shells may have drifted into a non-marine environment. However, most of these floaters were deposited in the strand zone and, therefore, embedded in near-shore sediments. In another paper (1957a) Reyment compares the color markings sometimes found on the aragonitic shells of Jurassic and Cretaceous ammonites with those of living *Nautilus* species and concludes that, in the former, color markings did not occur as rarely as is mostly assumed. A third paper (Reyment, 1959a) reports interesting observations on the septal apparatus and the siphuncle of 15 ammonite species, a few of them Jurassic but the majority Cretaceous; among the latter there is *Speetoniceras versicolor* Trautschold, subject of an earlier study by the same author (Reyment, 1956a; see Haas, 1958, p. 628).

A subject similar to the one discussed by Reyment (1958d) is treated by Géczy (1959b); this author, assuming that ammonite shells sink fast after the animal's death, excludes their transport over wide distances, as known in empty *Nautilus* shells. He concludes that in most ammonites, biotope and place of burial are more or less identical horizontally, though not vertically. In a somewhat earlier paper (1957) the same author refutes, on the strength of the literature of this century, Steinmann's and Beurlen's (compare above) hypotheses which ascribe an inner skeleton to ammonites.

Seilacher (1960) concludes from the mode of attachment of epizoic oysters to a Senonian *Buchiceras* from Peru that the ammonite's shell must have been external, that its adult stage lasted several years, and that *Buchiceras* was not benthonic but floated and swam close to the sea bottom.

Theobald (1958) deals with malformations in ammonites. Individual cases in nine species, all but one from the Jurassic, are described in detail. In summarizing his observations, the author distinguishes superficial and temporary lesions on the one hand and deeper ones on the other. The former account for distortion of ribs and other elements of the ornamentation but become resorbed later on. The latter cause considerable delay of growth of the costae, invasion of the affected flank by the opposite one, and disruption of bilateral symmetry. Internal lesions may affect sutural symmetry.

II

Only very few papers dealing with Triassic ammonoidea have lately come to the reviewers attention.

Bakalow, Kühn, and Sachariewa (1958) describe and illustrate the Lower Carnian fauna of Kotel, Bulgaria; in addition to some nautiloids, it includes ammonites of the genera and subgenera *Juvavites*, *Anatomites*, *Miltites*, *Paratibetites*, *Proarcestes*, *Joannites*, *Sphingites*, *Istreites*, *Cladiscites*, *Hypocladiscites*, *Megaphyllites*, *Mojsvarites*, *Diphyllites*, and *Placites*. Most of the species here recorded have been previously known from the Alps, from Hungary, from other localities of the Balkan peninsula, from the Himalayas, from Timor, and—just one species—from western North America. One species each of *Paratibetites* and *Istreites* and a subspecies of *Megaphyllites jarbas* are new.

From the Ladino-Carnian or earliest Carnian Arakura formation of Japan Nakazawa (1958) records a form believed to represent a new genus of the Monophyllitidae, provisionally named "*Monophyllites*" *arakurensis*, and a fragment doubtfully referred to *Monophyllites*. In a later paper (1959) the same author records from the Norian Nariwa group of Japan, in addition to a new species of *Germanonautilus*, an ammonite identified as *Arcestes* (*Stenarcestes*) sp. indet.

III

Much more numerous are recent studies on Jurassic ammonites. Here a new part of the *Fossilium Catalogus* by Zeiss (1959), covering the Hecticoceratinae, should be mentioned first. The other papers will be discussed in approximately geographic sequence.

Only a few among them deal with North

American faunas. In a paper on the Jurassic of Prince Patrick Island, Arctic Canada, Frebold (1957) describes and figures Toarcian to Lower Callovian ammonites referred to previously known or indeterminate species of the genera *Dactylioceras*, *Coeloceras*, *Pseudolioceras*, *Leioceras*, *Ludwigia*, *Cranocephalites*, and *Arctocephalites* and proposes a new genus, *Arkelloceras*, for *A. tozeri* Frebold, the type species, and *A. mclearni* Frebold. The new genus requires separation from *Cranocephalites* on the one hand and from *Garantia* on the other. Several faunules described by the same author (1959) from the Lower Jurassic of British Columbia contain two forms of *Arnioceras*, dated Sinemurian, two of *Harpoceras*, dated Toarcian, and a doubtful *Sonninia* that would indicate Bajocian age. A study on the Oxfordian of the Fernie group of Alberta and British Columbia by Frebold, Mountjoy, and Reed (1959) includes a paleontological section by Frebold with descriptions and photographs of ammonites of the genera *Cardioceras* (*Scarburgiceras*), *Cardioceras* s. str. and s. l., *Goliathiceras*, other cardioceratids and some fragments that could not even generically be identified. One *Cardioceras* species is new.

In his comprehensive paper on the Jurassic and Cretaceous stratigraphy and paleontology of Traill Ø, East Greenland, Donovan (1953) describes several Upper Bathonian to Lower Kimmeridgian ammonites, most of them referred to *Arctocephalites* (s. str. and subgenus *Cranocephalites*), others to *Kepplerites* (*Seymourites*), *Cardioceras*, *Amoebites* (s. str. and subgenera *Euprionoceras* and *Prionodoceras*), and *Arcticoceras;* among these forms three species, one with two varieties, another with one, and one variety are new.

In a paper establishing nine ammonite zones in the Middle Jurassic (?Bajocian to Lower Callovian) of East Greenland Callomon (1959) proposes a new species, *Cranocephalites indistinctus;* this species and six more that are selected as zone indices for the above mentioned nine zones except the top two are restricted to the Boreal province.

At the opposite end of the Americas, Alexander Land and the James Ross Island group, northeast Graham Land, have yielded the ammonite faunas dealt with by Howarth (1958). From the first area the Lower Kimmeridgian *Perisphinctes* (*Orthosphinctes*) *transatlanticus* Steinmann and Aptian forms of the genera *Phylloceras*, *Georgioceras*, *Sanmartinoceras*, *Ancyloceras* and *Silesites* are recorded, with a detailed description for *Sanmartinoceras patagonicum* only, from the second area Campanian forms of the genera *Tetragonites* (*Saghalinites*), *Desmophyllites*, *Maorites* (one new species), *Grossouvrites*, *Jacobites*, *Gunnarites*, and *Eupachydiscus;* most of these Campanian forms are described and well illustrated.

Of European ammonite assemblages, those of the Liassic of England, as monographed by T. Wright (1878–1886), have been revised and their nomenclature brought to date by Donovan (1954b); his systematic index of superfamilies, families, genera, subgenera, and species, although in part superseded by volume L of the Treatise, will be of great value to taxonomists. A work of similar magnitude and equal value is the same author's (1955) revision of the Lower Liassic ammonite species described in Reynès' unfinished monograph of 1879; here, too, the nomenclature is brought up to date; 11 of the species are excellently refigured. Still a third paper by Donovan (1958c), this one shorter and without illustrations, serves the purpose of revision of species established in the second half of the nineteenth century, namely of those of the Lower Liassic of the Bavarian Alps created by Gümbel. Another brief paper (1957) of Donovan's is devoted to a restudy of the Sinemurian species *Cymbites laevigatus* (Sowerby) from the Dorset coast and of Neumayr's genus to which it belongs.

The Middle Lias of the Dorset coast, divided into the two zones of (in ascending order) *Amaltheus margaritatus* and *Pleuroceras spinatum*, the first with three subzones, the second with two, is the subject of a paper by Howarth (1957); in its paleontological section eight species, none of them new, are described which belong to five families; four of these species are refigured.

In addition to the revisions listed above, two more papers are to be credited to Donovan that deal with faunas from the European continent. One of them (1958a) is a monograph of the Lower Liassic ammonite fauna from the Langeneckgrat near Thun, Switzerland, previously described by Hug (1899), but covers a larger material than did

Hug so that not all of the forms here described can be found in the earlier paper. The Juraphyllitidae are represented by a single specimen designated as *Juraphyllites* spec. nov.?, the Lytoceratidae by two species of *Lytoceras*, the Oxynoticeratidae by four species of *Oxynoticeras*, three of which are referred to Buckman's subgenus *Gleviceras*, by one species of *Radstockiceras* and by an indeterminate individual, the Echioceratidae by two species, one with a variety, of *Echioceras*, two of *Leptechioceras*, and seven of *Paltechioceras*, the Eoderoceratidae by three species of *Eoderoceras*, two of *Coeloderoceras*, one of *Crucilobiceras*, five of *Epideroceras*, two of them new, and one each of *Bifericeras* and *Coeloceras*, and the Polymorphidae by one form each of *Gemmellaroceras* (*Leptonotoceras*) and *Tropidoceras*. This paper is amply illustrated by both drawings and full tone plates. The other paper here to be mentioned (1958b), on the ammonite zones of the Toarcian "Ammonitico Rosso" of southern Switzerland and Italy, although primarily stratigraphic in scope, reviews about 35 forms, none of them new, which are referred to various genera of the Dactylioceratidae, Hildoceratidae, Graphoceratidae, and Hammatoceratidae.

In the same splendid Swiss series as Donovan, 1958a, appeared also, a few years earlier, the first part of a monograph by Maubeuge (1955) on the middle Jurassic (Aalenian to Bathonian) ammonites from the northern part of the Jura Mountains of Switzerland. In this part species of the families Tmetoceratidae (*Tmetoceras*), Hildoceratidae (*Staufenia*, *Pleydellia* with subgenus *Walkericeras*, *Cotteswoldia*, *Leioceras*, *Costileioceras* with subgenus *Canavarella*), Graphoceratidae (*Ludwigia* with subgenus *Apedogyria*, *Brasilia*, *Graphoceras* with subgenera *Pseudographoceras* and *Ludwigella*), Strigoceratidae (*Strigites*), Hammatoceratidae (*Parammatoceras*, *Euaptetoceras*, *Eudmetoceras*), Sonninidae (*Poecilomorphus*, *Sonninia*, *Witchellia* with subgenera *Spatulites* and *Maceratites*, *Dorsetensia*), Stephanoceratidae (*Stephanoceras*, *Normannites*, *Polyplectites*, *Docidoceras*), Otoitidae (*Emileia*), and Parkinsonidae (*Parkinsonia*) are described and beautifully illustrated. Three new species each are added to *Ludwigia* and *Poecilomorphus* and one to *Strigites* but, fortunately, no new generic or supgeneric names are proposed. A shorter paper of Maubeuge's (1957) is devoted to the detailed description and illustration of altogether 54 forms (in part just individual specimens and fragments) of the genus *Dactylioceras*, referred (without or with reservation) to 30 different species, eight of them new; in addition, a single fragment is tentatively referred to *Collina*. All these ammonites come from a single zone, that of *Dactylioceras semicelatum-tenuicostatum*, of the lowermost Toarcian of eastern France and Luxembourg.

Schirardin (1958), in turn, monographs the Oxfordian ammonites of the Ferrette area of Alsace. Among them the genera *Berniceras*, *Rossiensiceras*, *Putealiceras*, *Brightia*, *Campylites*, *Richeiceras*, *Taramelliceras*, *Creniceras*, *Quenstedtoceras* (s.str. and subgenera *Bourkelamberticeras*, *Vertumniceras*, *Pavlowiceras*, and *Eboraciceras*), *Scarburgiceras*, *Protocardioceras* (new, type species *Cardioceras praecordatum* R. Douvillè), *Anacardioceras*, *Cardioceras*, *Scoticardioceras*, *Pachycardioceras*, *Plasmatoceras*, *Properisphinctes*, *Prososphinctes*, *Alligaticeras*, *Discosphinctes*, *Parapeltoceras*, *Parawedekindia*, *Peltoceratoides*, *Prieserites*, *Rapailites*, *Euaspidoceras*, and *Paryphoceras* are represented. To many of the generic names just quoted, not to speak of the subgeneric ones, the reviewer would grant, at the most, only subgeneric rank. He was particularly interested to find among the many forms recorded in this monograph some of Noetling's and his own species from Mount Hermon, but somewhat disappointed to find, after all the pains he (1955, p. 101, 102) took to prove *Taramelliceras episcopale* (de Loriol) to be a junior synonym of *T. hermonis* (Noetling), this species still under de Loriol's name.

Hölder and Ziegler's paper of 1959 which bridges the French-German boundary is essentially a stratigraphic one but it also describes and figures some 20 Kimmeridgian ammonite species belonging to the genera *Perisphinctes* (s.l.), *Nebrodites*, *Sutneria*, *Aspidoceras*, *Hybonoticeras*, *Taramelliceras*, *Streblites*, *Neochetoceras*, and *Glochiceras*. The only *Nebrodites* species here described is new, as is the only *Glochiceras* species but the latter is credited to Berckhemer (in lit.).

Two subspecies, one of *Hybonoticeras*, the other of *Taramelliceras*, however, are credited to Berckhemer and Hölder, 1959, although that latter paper was published by Hölder (Berckhemer died in 1954) three months later than Hölder and Ziegler's.

Berckhemer and Hölder's 1959 paper is a comprehensive monograph of the Kimmeridgian ammonites from the upper "Weisser Jura" of southern Germany, discussing and beautifully illustrating forms belonging to the families Aspidoceratidae (*Aspidoceras*, *Hybonoticeras*), Perisphinctidae (*Perisphinctes* with subgenera *?Katroliceras*, *Virgatosphinctes*, and *Lithacoceras*, *Pavlovia*, *Lytohoplites*, *Sutneria*, and *Gravesia*), Oppelidae (*Taramelliceras*, with subgenus *Metahaploceras*, *Oxyoppelia*, *Ochetoceras*, *Neochetoceras*, *Haploceras*, and *Glochiceras*). One species and three subspecies of *Hybonoticeras*, two species of *Perisphinctes*, s.l., four species and four subspecies of *Taramelliceras*, three species of *Ochetoceras*, and one subspecies of *Neochetoceras* are new. The generic name *Oxyoppelia*, however, although not found in the Treatise, dates back to an earlier (1926) publication by Berckhemer.

Oechsle (1958) published a fine monograph on the stratigraphy and the Bajocian ammonite fauna of the Fils district of southern Germany. The careful description of altogether 25 species of the genus *Sonninia* Bayle is preceded by a thorough study of the morphology and mode of life of this genus and followed by a section on its descent, probably from *Ludwigia*. Despite the aforementioned great number of species the author, himself, proposes only one new specific name and favors a narrower circumscription of species than Dorn's (1935), relegating many species of earlier authors (Quenstedt, Brinkmann, Dorn, Hiltermann, Maubeuge) to subspecific rank and creating five new subspecies.

To Ziegler, mentioned above as coauthor of Hölder and Ziegler, 1959, we owe also several recent papers, all based on extremely careful studies of some Upper Jurassic ammonite assemblages, mostly from southwestern Germany. The earliest of these papers (1957) has for its subject a single species, the Kimmeridgian *Creniceras dentatum* (Reinecke); it is not only meticulously described, well illustrated and compared with its congeners *C. renggeri* (Oppel) and *C. crenatum* (Bruguière) but also its phylogeny, ecology, and stratigraphic and geographic ranges are examined. In the following year Ziegler (1958a) published an extensive monograph of the Oxfordian-Kimmeridgian genus *Glochiceras*. On the strength of the characters of the apertural margin he distinguishes within this genus, in addition to *Glochiceras* s. str., three new subgenera: *Coryceras*, *Lingulaticeras*, and *Paralingulaticeras*. All told, more than 30 species are recognized. The author bases his species concept strictly on morphology but interprets it elastically; the abundance of the material examined (more than 1700 specimens from southern Germany, Switzerland, and southern France) enables him, in most of the cases, to deal with populations rather than individuals. The evolutionary rates are found to be, in general, slow in this group. Ziegler, 1958b, is a comprehensive survey of the ammonites of the lower part of the "Malm Delta" (essentially the equivalent of the *pseudomutabilis* zone of the Kimmeridgian), with due regard to their "biochronology" and zoogeography. The same author's paper 1958c is essentially a stratigraphic investigation which, however, yields also valuable results concerning the evolution of two Lower Kimmeridgian ammonoid lineages, namely that of *Creniceras dentatum* on the one hand and that of *Sutneria cyclodorsata-S. eumela* on the other. The evolutionary changes taking place in these two lineages and in still a third, *Glochiceras*, this one reaching from the Upper Oxfordian up into the Middle Kimmeridgian, are the subject of a separate study by the same author (1959a). Another of Ziegler's papers (1959b) deals with the Upper Jurassic genera *Idoceras*, *Nebrodites*, *Simoceras*, and *Simosphinctes* (a genus established as recently as 1957 by Barthel) all of which are referred to Spath's subfamily Idoceratinae of the Perisphinctidae. Within *Simosphinctes* a new subgenus *Ceratosphinctes*, based on *Ammonites septenarius* Quenstedt, is established. An interesting result of this study is the observation of a case of dimorphism between macroconchs and microconchs, as first postulated by Callomon (see Haas, 1958, p. 625) for the

genus *Idoceras*, but such dimorphism is not granted general validity. It is worth noting that, within the group, only the micromorphs have "ears" (lateral lappets), a fact that may indicate sexual dimorphism. The large plate accompanying the last paper deserves special praise for its excellent photography.

Géczy, mentioned above for two papers of a more general scope, attempts in a brief article (1958) a quantitative evaluation of more than 6500 ammonites, mostly phylloceratids and lytoceratids, from Csernye in the northern Bakony Mountains of western Hungary, ranging in age from Middle Liassic to Middle Dogger. Their abundance is found gradually to increase with time, whence the author infers an increase in the depth of the sea. A specimen from the same Bakony Mountains, of Pliensbachian age, is made by Géczy (1959a) the type of a new species which, in turn, is designated the type species of a new subgenus, *Hemiparinodiceras*, of *Liparoceras*.

Another Hungarian author, Kaszap (1959), lists and illustrates, in the course of a study of the Dogger (Bathonian-Callovian) beds of the Villany Mountains of southern Hungary, a considerable number of ammonite species belonging to the genera *Phylloceras*, *Calliphylloceras*, *Holcophylloceras*, *Ptychophylloceras*, *Sowerbyceras*, *Lytoceras*, *Oxycerithes*, *Hecticoceras* (*Putealiceras*, *Brightia*, *Rossiensiceras*, and *Lunuloceras*), *Prohecticoceras*, *Kosmoceras*, *Lissoceras*, *Grossouvria*, *Subgrossouvria*, *Procerites*, *Prososphinctes*, *Poculisphinctes*, *Indosphinctes*, *Wagnericeras*, and *Choffatia*.

In the recent Italian paleontological literature we find a memoir by Vialli (1959) on the Sinemurian ammonites of the Monte Albenza, province Bergamo; they belong to the Juraphyllitidae (*Juraphyllites*), Phylloceratidae (*Paradasyceras*, *Geyeroceras*), Ectocentritidae (*Ectocentrites*), Schlotheimiidae (*Schlotheimia*, *Charmasseiceras*, *Boucaulticeras*), Arietitidae (*Arnioceras*, *Pararnioceras*, *Arietites*, *Coroniceras*, *Eucoroniceras*, *Vermiceras*, *Euagassiceras*, *Agassiceras*), Alsatidae (*Pseudotropites*), and Eoderoceratidae (*Eoderoceras*). A paper by another Italian author, Cassinis (1957), deals with aptychi of the genera *Lamellaptychus* and *Punctaptychus* from the Prealps of the province of Brescia; one of the species described is dated Kimmeridgian and one Kimmeridgian-Tithonian, while the others range in age from Tithonian to Hauterivian, perhaps Barremian.

In addition to his papers already reviewed above (p. 581) and his many contributions on Cretaceous ammonites Reyment has also a paper on Jurassic ammonites (1959b) to his credit, namely on members of the genera *Coroniceras* (*Primarietites*), *Megarietites*, *Paracoroniceras*, *Agassiceras*, *Euagassiceras*, *Arnioceras*, *Eparietites*, *Cymbites*, *Oxynoticeras*, *Promicroceras*, *Polymorphites* (s. str. and subgenus *Uptonia*), and *Dactylioceras*, ranging in age from Sineumrian to Toarcian, from Skåne in southern Sweden. Most of the accompanying photographs are outstanding in clarity. The association of the ammonites with plant remains is interestingly discussed and interpreted ecologically.

Having disposed of the literature on American and European occurrences of Jurassic ammonites, we now have just two papers on African ones to review. First is Venzo's (1959) monograph on late Jurassic (almost exclusively Kimmeridgian) ammonites from the high plains of Harrar province, Ethiopia. It is essentially a revision of an earlier paper (1942) with nearly the same title; the plates are entirely unchanged. The fact that the earlier issue had been published, under wartime restrictions, in only 200 copies, made republication desirable. Furthermore, revision of the text serves mainly the purpose of the integration, first suggested to the author by this reviewer in 1948, of a study of the Jurassic ammonites of the same area undertaken independently, but published only a year after Venzo's, by Scott (1943). In his introduction Venzo lists 13 of Scott's forms that are also represented in his material, among them six for which Scott had proposed new specific names. Surprisingly, however, four of these species of Scott's are explicitly maintained as valid by Venzo and one tacitly; only one of them is considered a synonym of an older species of Dacqué's. If the occurrence of the forms studied by both authors in the same area and, in some cases, even at the same locality is taken into account, the fact just mentioned should suggest a rather narrow circumscription of species. Venzo describes

and illustrates forms of the genera *Biplices, Pachyplanulites, Dichotomosphinctes, Ataxioceras, Lithacoceras, Planites, Enosphinctes, Torquatisphinctes, Subplanites, Katroliceras, Idoceras, Waagenia, Nebrodites, Aspidoceras, Physodoceras,* and *Simaspidoceras;* none of these generic names is new but altogether eight new specific ones are proposed, all but one dating back to the earlier edition of 1942.

To Collingnon (1958, 1959) we owe hitherto four—as far as the reviewer knows—fascicules of his atlas of characteristic fossils from Madagascar. They consist of 95 plates, some of them unfortunately, too pale, depicting Jurassic ammonites from that island. Unfortunately, I have not had an opportunity to see the two first fascicules which are devoted to Liassic to Bajocian and to Bathonian ammonites, respectively. The third fascicule illustrates Oxfordian, and the fourth Argovian-Rauracian forms. Not all of these have been previously known; many new species and varieties are named and described in the explanations of the plates and even a new subgenus of *Idoceras, Praeidoceras,* is there proposed for *I.* (*P.*) *madagascariense* Collignon.

Turning now from Africa to Asia, we find the ammonites of the famous Jurassic fauna of Kutch, previously monographed by Waagen (1873–75) and Spath (1927–33), once more as the subject of a study, this time by Agrawal (1956) who has to his credit also some earlier stratigraphic papers and a later one (1957) on those beds. The last mentioned paper deals also with their fauna, including the ammonites, without, however, illustrating them. Therefore, for the purpose of this review, attention may be focused on the 1956 paper. Only the major portion of Chapter III of this extensive work is devoted to the Ammonoidea. Forms of the genera *Caliphylloceras, *Ptychophylloceras* (a new species), *Subbonarellia, Putealiceras, Streblites, Macrocephalites, *Indocephalites, *Kamptokephalites, *Dolikephalites, Eucycloceras, *Subkossmatia, Pachyceras, *Mayaites, *Epimayaites, *Dhosaites, *Paryphoceras, *Reineckia, *Kellawaysites* (one new species), **Reineckeites, *Obtusicostites, *Kinkeliniceras* (one new species), **Hubertoceras, *Subgrossouvria, Otosphinctes, Perisphinctes, Pachyplanulites, Peltoceras, *Metapeltoceras, Peltoceratoides,* and **Euaspidoceras* are listed and, in part, described; those preceded by an asterisk are also illustrated.

From Japan, three papers dealing with Jurassic ammonites have reached the reviewer. Two of these are by Sato. The first (1957) is chiefly concerned with the biostratigraphy of the Hettangian to Aalenian Shizukawa series of northern Japan; this series is split up into six zones. The results thus obtained are then correlated, on the strength of the ammonite faunas, first with the stratigraphy of the contemporaneous beds of all circumpacific areas, including those of the Americas, then with the European standard. One chapter of this paper only is devoted to the paleontology; here seven species referred to the genera *Holcophylloceras, Phylloceras, Kallilytoceras, Arnioceras, Harpoceras,* and *Hyperlioceras,* none of them new, are described and figured. Sato's second paper (1958) adds to the knowledge of the fauna of the same series by creating a new genus *Hosoureites,* based on *Harpoceras ikianum* Yokoyama as its type species, in the family Graphoceratidae and by describing, in addition to that species, three *Graphoceras* species which are left undetermined. The third of these Japanese papers dealing with Jurassic ammonites is by Matsumoto (1956); in it he establishes a new genus *Yebisites* (Psiloceratidae, Alsatitinae), type species *Y. onoderai* Matsumoto from the lower part of the Shizukawa group, probably Hettangian in age, of northern Japan.

IV

The bibiography of the most recent literature on Cretaceous Ammonoidea lists perhaps not quite as many titles as that on Jurassic ones but the papers here to be reviewed are certainly in no way inferior in significance. Here, too, an approximately geographic sequence will be followed, this time starting in Europe and going from there westward around the globe.

Sarkar (1955) devotes a most careful and amply illustrated study to the "ammonites déroulés" (perhaps best translated "loosely coiled and uncoiled ammonites") of the Lower Cretaceous of southeastern France. In two preliminary papers (1954a,b) the author had proposed seven new generic

names; of these, however, only *Balearites* (type species *Crioceras balearense* Nolan) has been accepted by Wright (1957) for the Treatise, while four more, *Emericiceras*, *Dissimilites*, *Escragnolleites*, and *Moutoniceras* are there considered synonyms, or doubtful synonyms, of preexisting generic names and two more, *Jaubertites* and "*Sapthicrioceras*," are rejected as *nomina nuda*. Meanwhile Sarkar, in his aforementioned monograph, had replaced *Jaubertites* by *Jauberticeras* (type species *J. dubius*, should read *dubium*, Sarkar), unaware that he thus created a homonym of *Jauberticeras* Jacob, 1907, and the—misspelled—"*Sapthicrioceras*" by *Spathicrioceras*, type species *S. sornayi* Sarkar. In addition to these two new (as of 1955) generic names, he also proposed a new subgenus of *Acrioceras* Hyatt, *Protacrioceras*, type species *Ancyloceras ornatum* d'Orbigny, 1840. The reviewer does not venture to pass judgment on the validity of these three additional supraspecific names, aside from recognizing *Jauberticeras* to be a homonym, but the fate of their seven predecessors of 1954 does not bode too well for them. In addition to those altogether ten supraspecific names, Sarkar (1955) also proposes altogether 72 new specific ones and a considerable number of new varieties in addition. However, the number of individuals made the hypodigm of a description is never given. From this and other indications it must be suspected that the author gives, in most cases, descriptions of specimens rather than of species; thus, his approach appears to be a strictly typological one. The photographs illustrating this monograph are excellent.

To Basse de Menorval and Sornay (1959) we owe a series of most informative surveys of the Upper Cretaceous ammonite faunas of France, the latter author treating those of the Cenomanian and Maestrichtian, the former those of the Turonian, Coniacian, Santonian, and Campanian. Two important observations on the Cenomanian should be quoted: Sornay considers the change in ammonite faunas at the Albian-Cenomanian boundary the most marked one in the post-Triassic Mesozoic; to him it indicates the beginning of a decrease in numbers of both individuals and of species and genera that eventually leads to the extinction of the whole subclass of the Ammonoidea. Furthermore, he notes a marked faunal difference between two regions of France, the Paris Basin, the North, and the Charentes on the one hand and the Southeast on the other, with the former showing close affinities to the Cenomanian of England and Germany, the latter exhibiting a mediterranean aspect. Similarly, Basse distinguishes two marine provinces in the Turonian: a northern one, comprising the Ardennes and the Parisian and Aquitanian basins, and a southern one, comprising the northern slope of the Pyrenees and the alpine regions. The Aquitanian basin, however, can in certain respects be joined to the southern province as well, despite its close faunistic affinities to the other regions of the northern one. Because of the absence of major diastrophism there is biostratigraphic continuity in the northern province. The same two provinces are distinguished in the Senonian (Coniacian, Santonian, Campanian) also, with the northern one subdivided into the Paris basin and the Aquitanian one. In Maestrichtian time there occurs a considerable reduction of marine beds with ammonites; they are now found in four areas only. Their faunas show the closest relationship with those of northern Europe and of the northern Alps. The enumerations and critical discussions of many genera and species found in every one of these four surveys cannot possibly be entered into in the present review.

Jost Wiedmann, a disciple of Schindewolf, makes his debut in ammonite literature with an interesting study of the Upper Cretaceous of Spain and Portugal and of its cephalopods (1959). It is this paper's paleontological appendix that most interests us here. Here a new subfamily of the Vascoceratidae, the Fallotitinae, and altogether ten new generic and subgeneric names are proposed, namely, *Lotzeites*, a subgenus of *Calycoceras*, *Proromaniceras*, a subgenus of *Romaniceras*, and the genera *Schindewolfites* and *Jeanrogericeras*, all these in the Acanthoceratidae, *Fallotites*, with a subgenus *Ingridella*, and *Spathitoides*, a subgenus of *Neoptychites*, in the Vascoceratidae, *Donenriquoceras* and *Reymentoceras*, a subgenus of *Tissotioides* (see below), in the Tissotiidae, and *Ciryella*, a subgenus of *Gauthiericeras*, in

the Collignoniceratidae. The reviewer cannot claim that he checked the differences from previously known genera and subgenera on which the author bases the separation of his new ones thoroughly enough to pass judgment as to whether or not these separations may be justified but he cannot help feeling that at least some of those differences should not be granted higher than interspecific rank.

The fundamental work for the knowledge of the ammonites of the Upper Cretaceous Gosau beds of the northern calcareous Alps of Austria has always been Redtenbacher's monograph of 1873; it has also constituted a very important source of reference for workers on more or less contemporaneous, that is, Coniacian, ammonites from other areas. However, since Redtenbacher, except for the species referred to *Hamites* and *Scaphites*, still used indiscriminately the genus designation "*Ammonites*," his paper was bound to become antiquated as time went on. A revision was first attempted by Brinkmann in 1935 but the years since then have seen a tremendous amount of newly created generic and subgeneric names. Now Reyment (1958b) has brought the taxonomy up to date, proposing, in the course of this procedure, a new genus, *Tissotioides*, based on *Ammonites haplophyllus* Redtenbacher as type species. The author points out that the new genus is a homeomorph of *Barroisiceras* but that—as in other cases (see Haas and Simpson, 1946, p. 339)—this homeomorphy can be unmasked by having recourse to the suture lines which have entire, tissotiid saddles in *Tissotioides* but deeply indented ones in *Gauthiericeras* (compare text-figs. 2/1 and 6/1,2 of this paper). A particular merit of this revision is that it is accompanied by excellent photographs of all of Redtenbacher's originals that are still available and by many suture line drawings; for the older author's original figures and drawings proved to be not entirely reliable. Reyment also gives a revised diagnosis of *Barroisiceras* s.str.

Another paper that, like Sarkar's monograph mentioned above, was published in 1955 but is covered only in this part of our review, is Sornay's on Cretaceous ammonites from the Mellègue Mountains of Algeria. It is the first among those here reviewed that has an African fauna for its subject. Here altogether nine new species and five new varieties belonging to the genera *Scaphites*, *Idiohamites*, *Parahoplites*, *Acanthoplites*, *Hypacanthoplites*, *Acompsoceras*, *Cottreauites*, and *Prionocycloides* are proposed; using open nomenclature, the author records also forms referred to *Gaudryceras*, *Protanisoceras*, and *Aconeceras* and leaves two specimens undetermined even generically. The age of this fauna ranges from Barremian to Coniacian. It is amply and well illustrated.

Another study of a North African fauna, of Upper Cretaceous age, has for its author Collignon (1957) whom we meet for the first time in this part of Africa. In addition to the ammonites three nautiloid species are here recorded, one occurring in the Cenomanian and two in the Upper Maestrichtian. Of the ammonoid genera, *Neolobites* is represented in the Cenomanian; *Nigericeras*, *Mammites* (one new variety), *Vascoceras* and its subgenera *Paravascoceras* (one new species) and *Discovascoceras* (new, type species *D. tesselitense*, new), *Hoplitoides*, *Pseudotissotia*, *Bauchioceras*, *Furoniceras* (new, type species *F. trumpyi*, new), and *Leoniceras* are recorded from the Lower Turonian and *Libycoceras* from the Upper Maestrichtian. At all three horizons the faunas exhibit a typically Tethyan aspect.

In the years since 1957 Reyment has added several more important contributions to the knowledge of the Upper Cretaceous ammonites of Nigeria and the Cameroons to those previously (Haas, 1958, p. 627, 628) reviewed. In the first of these papers (1957b) he infers from the occurrence of an ammonite identified as *Texanites* aff. *hourqui* Collignon the presence of the Lower Santonian in northeastern Nigeria. In a larger contribution (1957c)* Reyment creates six new species and a new subspecies in the ammonite genera *Acanthoceras*, *Sphenodiscus*, *Watinoceras*, *Coilopoceras*, *Peroniceras*, and *Dipoloceras*. The new *Peroniceras* species, *P. quadrituberculatum*, is made the type species of a new subgenus *Reginaites*. In

* The reviewer would prefer its title to read "Ueber einige fossile Wirbellose . . ." rather than "Ueber einige wirbellose Fossilien. . . ." A single Dinosaur femur is "wirbellos" but still part of a fossil vertebrate, not invertebrate.

addition to the genera mentioned, *Acompsoceras*, *?Gauthiericeras*, *?Calycoceras*, *Turrilites*, *Gyaloceras*, *Oxytropidoceras*, *Pachydiscus*, and *Desmoceras* are represented. The chronological range of all these ammonites extends from Middle Albian to Upper Maestrichtian. I cannot help praising the views of the holotype of *Dipoloceras hausa* Reyment (pl. 8, figs. 1a,b) as two of the most beautiful photographs of ammonites I have ever seen. Still another of Reyment's papers dealing with the Cretaceous of Africa (1958c) serves a purpose similar to that of his paper 1958b (see above); here it is Solger's monograph of 1904 on the fossils of the Cretaceous Mungo beds of the Cameroons whose taxonomy is brought up to date. Most of Solger's originals, as far as they are still availabe, are refigured in clear photographs. As now revised, the Mungo fauna includes members of the following ammonite genera: *Pachydesmoceras*, *Benueites*, *Kamerunoceras*, *Watinoceras*, *Neoptychites*, *Choffaticeras*, and *Hoplitoides* of the Turonian, *Baculites*, *Tissotia*, *Peroniceras*, *Solgerites*, *Dordiella* (new, type species *D. bakundu* new species), and *Forresteria* of the *Coniacian*, *Texanites* and *Pseudoschloenbachia* of the Santonian. The ontogeny of a new species of the last genus, *P. bakwerri*, suggests to the author a possible relationship of this genus with the Collignoniceratidae, especially with their subfamily Barroisiceratinae.

Switching now to the Americas, we discuss first two papers by Donovan dealing with Cretaceous ammonites from Greenland. The first of these (1953) has already been reviewed above (p. 583), as far as it is concerned with Upper Jurassic Ammonoidea. Here it remains to discuss that part of it that is devoted to Cretaceous ones. The latter comprise a Valanginian *Phylloceras* and two *Lytoceras* species, one also Valanginian, the other Aptian. The genus represented by the greatest number of species, however, is the middle Valanginian *Polyptychites* with nine species, one of them new, referred to *P.* s. str. and three more, all new, to the subgenus *Euryptychites*. Other genera present of the same age are *Dichotomites* (one new variety) and *Neocraspedites* (two new species). From the Aptian a species of *Sanmartinoceras* is recorded, from the Albian a new species of "*Puzosia*" and one new species each of *Arcthoplites* and *Leymeriella* and an indeterminable doubtful mortoniceratid. Of Upper Cretaceous stages the Cenomanian has yielded three forms of *Schloenbachia*, the Turonian two species of *Scaphites*, and the Campanian two more forms of this genus, one of them new. Another paper by Donovan (1954a) describes and illustrates Upper Cretaceous ammonites from East Greenland, namely, one species each of *Phylloceras*, *Lytoceras*, and *Gaudryceras* and six species of *Schloenbachia* from the Cenomanian, a doubtful *Collignoniceras* from the Turonian, and the new *Scaphites* species just mentioned, *S. greenlandicus* Donovan, from the Campanian.

Proceeding to the American continent, we begin with the Texas Cretaceous. On this, two more contributions by Young can be listed (see Haas, 1958, p. 630, 631). One of them (1958a) revives the generic name *Graysonites* Adkins, a *nomen nudum*, for a group of Lower Cenomanian acanthoceratids, split into four new species: *G. lozoi*, the type species, and three more, one of them previously recorded as *Acanthoceras* aff. *cunningtoni* by Böse and Adkins. Young's other paper (1958b) describes a faunule from Trans-Pecos Texas consisting of members of the genera *Hypoturrilites*, *Ostlingoceras*, *Neopulchellia*, *?Utaturiceras*, *Metoicoceras*, *Watinoceras*, and *Pseudouhligella*; the *Metoicoceras* is dated Lower Turonian, the other forms Cenomanian, the older ones among them believed to have been redeposited. Four among the Cenomanian genera, viz., *Hypoturrilites*, *Ostlingoceras*, *Neopulchellia*, and *Pseudouhligella*, are new to Texas.

Clark (1958) discusses records of *Anisoceras* and *Ancyloceras* from Texas and reaches the conclusion that only the first genus is there represented by three species, one of them new. In another paper (1960) the same author proposes a new species of *Parapuzosia* (*Austiniceras*) from the (Upper Turonian) Eagle Ford formation of Dallas County. His holotype, the only specimen, although septate throughout, measures 600 mm. in diameter and must have attained considerable size when complete, perhaps even one comparable to that of the enormous disks, attaining diameters of up to

more than 1.4 m., of the same genus recorded by Scott and Moore (1928) from the Del Rio road near Eagle Pass, Texas.

A small assemblage of Lower Turonian (or uppermost Cenomanian) age from Arizona, consisting of species of the acanthoceratid genera *Metoicoceras*, *Calycoceras*, and *?Dunveganoceras*, is described and amply illustrated in a third paper by Young (1957); all the species are considered new but only those referred to the two first genera are named.

Cobban's many valuable contributions on Upper Cretaceous Ammonoidea from the western interior of the United States have erroneously been omitted in the first part of this review. They are now included here, along with a later paper of his. Perhaps most important among those earlier papers is his beautifully illustrated study of the scaphitoids from the Greenhorn, Carlile, and Niobrara formations of the Colorado group (1951a) in which 49 forms, 34 of them new, are carefully described and separated from one another. Of those 49 forms 39 are referred to *Scaphites* s. str., nine (six species, three of them with one variety each) to a new genus, *Clioscaphites*, based on *C. montanensis* Cobban as its type species, and one to *Desmoscaphites*. Three shorter papers by this author deal with baculitids; two of them (1951b, 1958) erect five new species of *Baculites* which, along with other species of this genus, constitute valuable indices for zones of the Upper Colorado and Montana groups; a third (1952) proposes a new genus, *Pseudobaculites*, for *P. nodosus* Cobban, the type species, and *P. wyomingensis* Cobban. A more comprehensive paper (1953a) has for its subject the Cenomanian ammonites of the genera *Metoicoceras* (two new species) and *Dunveganoceras* (one new species, one new subspecies) of the Mosby sandstone of central Montana. In 1953b Cobban records a new species of *Prionocyclus*, *P. quadratus*, from the Upper Carlile shale of Montana and South Dakota, and in a joint paper with Rohrer and Erdmann (1956) the Turonian species *Collignoniceras woollgari* (*forma typica* and varieties *regularis* and *intermedia*) from a locality in Toole County, Montana.

A considerable amount of new literature deals with Cretaceous ammonite assemblages from the Pacific border of North America. Starting high in the North, we encounter there the first of the results of Matsumoto's most successful "invasion" of the United States for the purpose of correlation of American and Japanese knowledge on Cretaceous ammonites. This is his study on Cretaceous (Cenomanian) ammonites from Alaska (1959a). Altogether 17 species, four or possibly six of them new, of the families Phylloceratidae (*Partschiceras*, *Neophylloceras*), Desmoceratidae (*Desmoceras*, *Pachydesmoceras*), Kossmaticeratidae (*Marshallites*, *Eugunnarites*, and *Maccarthyites*, new, type species *M. gracilis* Matsumoto), Placenticeratidae (*Proplacenticeras*), Tetragonitidae (*Parajaubertella*, *Anagaudryceras*, *Zelandites*, and *Tetragonites*), and Anisoceratidae (*Anisoceras*) are described and beautifully illustrated.

Also from Alaska are four new genera, established by Imlay (1959); three of them, *Moffitites*, *Freboldiceras*, *Kennicottia*, are referred to the subfamily Puzosiinae of the Desmoceratidae, the fourth, *Parasilesites*, to the family Silesitidae. Here again, as in the case of Wiedmann (p. 588) the reviewer wonders if their differences from previously established genera are wide enough to justify creation of new ones. A similar doubt is expressed by Howarth (1960) concerning the differences of the perisphinctid genus *Homolsomites* Crickmay, 1930, explicitly maintained by Imlay (1956), from *Neocraspedites*. "*Homolsomites*" is Valanginian in age and ranges from California through Oregon and Washington to British Columbia; according to Imlay, it occurs also in Greenland. In a third paper (1957) Imlay proposes three more new generic names for Hauterivian ammonites from California and Oregon: *Hannaites*, a berriasellid, and *Wellsia*, *Hertleinia*, since emended (Imlay, 1958) to *Hertleinites*, and *Hollisites*, all olcostephanids. Here, too, I feel some doubts as to the necessity of the creation of these new generic names.

In 1958 the great monograph by the late F. M. Anderson on the Upper Cretaceous (Albian to Maestrichtian Danian) of the Pacific Coast, dating back to the early forties, was finally published under the editorship of J. Wyatt Durham. Only about one-fourth of this paper (p. 180–273) is devoted to the ammonites of the region. The date of

the editorial preface (April 17, 1950) explains to a certain extent that the nomenclature is here and there somewhat outdated. For example, the author was ignorant of the fact that the name *Cyrtochilus* Meek, 1876, is a junior homonym of *Cyrtochilus* Jakowlow, 1875, and has, therefore, had to yield to its objective junior synonym *Sciponoceras* Hyatt, 1894, which is based on the same type species, *Hamites baculoides* Mantell, or of the substitution by Breistroffer, for similar reasons, of the name *Collignoniceras* for *Prionotropis*. As might be expected, many new specific names are proposed and also a subgeneric one and six generic ones. However, none of these seven supraspecific names is likely to survive the revision of Anderson's taxonomy by Matsumoto (1959–1960). Five of them are there with certainty considered synonyms, namely, *Neokotôceras* (type species *N. fresnoense* Anderson, Campanian or Maestrichtian) of *Damesites* Matsumoto, *Joaquinites* (type species *J. fascicostatus* Anderson, same age) of *Pachydiscus* s. str., *Butticeras* (type species *B. buttense* Anderson, Campanian) of *Submortoniceras* Spath, *Oregoniceras* (type species *Schloenbachia oregonensis* Anderson, Turonian) of *Subprionocyclus* Shimizu (see also Wright, 1957, p. L427), and *Eocanadoceras*, proposed as a subgenus of *Puzosia* (type species *E. hannai* Anderson, Turonian) of *Jimboiceras* Matsumoto, and two more doubtfully, viz., *Neocyrtochilus* (type species *N. bryani* Anderson, based on a very poor specimen, Upper Campanian) of *Polyptychoceras* Yabe and *Exicrioceras* (type species *E. ortigalitense* Anderson, Maestrichtian) of *Exiteloceras* Hyatt. The need for such taxonomic and nomenclatural emendation does, however, in no way impair the lasting value of Anderson's monograph; the stratigraphic section and those parts of the paleontological one that are concerned with invertebrates other than Ammonoidea are not affected by Matsumoto's revision; as far as the ammonites themselves are concerned, the careful descriptions, meticulous data on occurrence, and abundant illustrations are bound to be of great assistance to future students.

Matsumoto's monumental monograph on Upper Cretaceous ammonites of California (1959–1960) which, as just mentioned, supersedes Anderson's, was published in three parts; the first is devoted to the baculitids, the second to all other ammonoids, and the third to the stratigraphy and the conclusions. The ammonites here studied range in age from Upper Albian to Maestrichtian. It is somewhat surprising to find only two new species of *Baculites* and one renamed species of *Acanthoceras* proposed in a work of this scope. This is obviously due to the many earlier studies on this fauna and related ones. This reviewer derives even more satisfaction from the fact that, in contradistinction to so many much shorter papers here reviewed and also to earlier papers by the same author, not a single new generic name is here proposed. (The author suspects one form doubtfully referred to *Eucalycoceras* to represent a new genus but wisely refrains from naming it.) An extreme refinement of the stratigraphic sequence of the ammonite faunas of California and the realization of their intimate connections with those of Japan must be counted among the most valuable results of this work.

Before leaving the Pacific coast of North America, we mention a paper by Murphy and Rodda (1959) on one new species each of the genera *Desmoceras* (*Pseudouhligella*) and *Cleoniceras* from the Albian of northern California.

A paper by Imlay (1954) on Barremian ammonites, mostly juveniles, of the genera *Phylloceras, Lytoceras, ?Hamulina, ?Ancyloceras, Leptoceras, Melchiorites, ?Barremites, ?Saynoceras, Pulchellia, Karstenia,* and *?Nicklesia* from Trinidad, B.W.I., is here mentioned only belatedly.

A few papers deal with South American Ammonoidea. Leanza (1958) describes, and dates as Upper Valanginian, four species (two represented by two specimens each, the two others by only one specimen each) of the typically boreal genus *Simbirskites* from Argentina. It is worth noting that, in this paper, the author considers ammonites in general less useful than other fossils for paleozoogeography, mainly because ammonite sequences in a given basin may be interrupted by stratigraphic gaps.

The three other papers on South American ammonoids are devoted to ammonites from Colombia (and Venezuela). In his biostratigraphy of the Sabana de Bogotá

Bürgl lists and illustrates many Berriasian (including some dated Upper Tithonian by him) to Maestrichtian forms from an area extending over a large section of Colombia. Some of these are also described and figured by Haas (1960) among 48 from the Cordillera Oriental which range in age from Lower Berriasian to Barremian. The families represented are Ancyloceratidae, Ptychoceratidae, Haploceratidae, Perisphinctidae, Olcostephanidae, Berriasellidae, Desmoceratidae, Holcodiscidae, Pulchelliidae, and Douvilleiceratidae. *Olcostephanus*, *Berriasella*, *Substeueroceras*, *Thurmanniceras*, *Favrella*, *Sarasinella*, *Acanthodiscus*, *Pseudoosterella*, and *Nicklesia* are the most abundant or otherwise important genera. Many species are considered new but only twelve among these are named. Among those, *Substeueroceras mutabile* is remarkable for the thorough changes it undergoes in its ontogeny. The small genus *Pseudoosterella* has previously been known only from Europe. A single individual closely resembles the rare *Holcodiscus camelinus* (d'Orbigny) from Escragnolles (southern France). A postscript to this paper notes the close similarity between some of these Colombian forms and some described and figured by Sato (1958, see below) from Japan. Coniacian ammonites from Colombia and the adjacent Maracaibo area of Venezuela constitute the subject of the last of the many papers by Reyment (1958a) covered by the present review; they are referred to the genera *Baculites*, *Niceforoceras*, *Reesidites*, *Prionocycloceras*, *Forresteria*, and *Paralenticeras* (one species, new).

Howarth's (1958) work on Cretaceous ammonites from Alexander Land and Graham Land has already been discussed above (p. 583).

On the other side of the Pacific, Glaessner (1958) records several ammonite species, referred to the genera *Chimbuites* Casey and Glaessner (new, type species *Ch. sinuosocostatus* Casey and Glaessner), *Puzosia*, *Myloceras*, and *Labeceras*, from the Albian of New Guinea. The diagnosis of the new genus is given by Casey who places it in the Hoplitidae, close to *Puzosigella* Casey, *Lemuroceras* Spath, and *Cymahoplites* Spath, and also notes its similarity to *Pachydesmoceras* and *Uhligella* of the Desmoceratidae.

Perhaps owing to Matsumoto's recent concentration on Alaskan and Californian ammonite faunas, the literature on Japanese ones is represented in this part of our review by markedly fewer titles than in the first. Still, two more papers by that author can here be mentioned. One (Matsumoto, 1957) describes and illustrates a new species of *Damesites*, *D. ainuanus*, from the Turonian of Hokkaido, the other (Matsumoto, 1959b) is essentially concerned with the zonation of the Upper Cretaceous of Japan but, because of its line drawings of desmoceratid, pachydiscid, and kossmaticeratid species serving as zonal indices, also constitutes a valuable contribution to ammonite study. Jointly with Saito and Fukada, Matsumoto (1957) devotes Part XI of the series on Cretaceous ammonites from Hokkaido and Saghalien to the Acanthoceratidae from Hokkaido. In that area this family is represented by the previously known genera *Mantelliceras*, *Calycoceras*, *Romaniceras*, *Acanthoceras*, *Euomphaloceras*, and *Protacanthoceras;* in addition, a new genus, *Yubariceras*, closely related to *Acanthoceras* and *Romaniceras*, is proposed for *Y. yubarense*, the type species, and two more forms. As far as the age of these ammonites could be ascertained, it ranges from Paleogyliakian (Upper Cenomanian) to Neogyliakian (Turonian). Sato (1958b) proves, by records of the genera *Olcostephanus*, *Thurmanniceras*, *Kilianella*, and *Berriasella*, the presence of the Berriasian on the Kitakami plateau of northern Japan. The striking similarity of some of his forms to Colombian ones of about the same age has been mentioned above.

By way of appendix to this review of the latest Japanese literature on ammonites two papers by Obara are mentioned here, although the first of them (1959), on the relative growth in some desmoceratids, does not deal exclusively with Japanese specimens. Here the author reaches the conclusion that relative growth in all species examined follows, in general, the same rule but that all the same every species exhibits its particular mode of growth. The second paper (Obara, 1960) is devoted to a mathematical analysis of the spiral in some ammonites of the families Phylloceratidae, Tetragonitidae, and Desmoceratidae; here, too, a general equation is arrived at but peculiari-

ties according to family are recognized and variations in the course of the ontogeny are observed in some species.

POSTSCRIPT.—Only after conclusion of this essay-review did I see Chao Kingkoo's (1959) extensive monograph on Lower Triassic ammonoids from the Chinese province of Kwangsi but I have not yet had an opportunity to study it. I intend to review it at some later date.

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PLEISTOCENE BIGHORN SHEEP FROM THE GREAT BASIN

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ABSTRACT—Partial skulls of 15 bighorn sheep mostly from Pleistocene lake deposits near Salt Lake City have been measured and compared with living forms from North America and the Old World. The Great Basin specimens all belong to one species and are referred to *Ovis catclawensis*, Hibbard and Wright, previously known only from a fragmentary jaw from Mohave County, Arizona. *Ovis catclawensis* resembles *Ovis ammon* from the High-Asian plateaus more than it does the living North American species, *Ovis canadensis*. Details of bighorn migrations between North America and Eurasia are not yet fully understood.

INTRODUCTION

REMAINS of about 15 Pleistocene bighorn sheep have been accumulated in collections of the Department of Geology, University of Utah. Practically all the specimens consist of one or two horn cores attached to posterior cranial elements. A few loose teeth, vertebrae and limb bones are also represented. Most of the specimens were found in the Hardman Gravel Pit in the foothills of the Wasatch Range in northeastern Salt Lake City; a few came from other gravel pits at the same geological level and one specimen was discovered beneath a Pleistocene volcanic ash bed in the East Humboldt Range near Winnemucca, Nevada. (See text-fig. 1 for localities.)

ACKNOWLEDGMENTS

The thoughtfulness of owners and operators of local gravel pits in preserving and donating specimens of the bighorn sheep is hereby acknowledged. Persons who have made comparative material available include Dr. S. D. Durrant, Department of Zoology, University of Utah; Miss Dee Ann Suhn, Department of Anthropology, Unisity of Utah; and Dr. D. H. Johnson, U. S. National Museum. Their assistance is appreciated. Helpful suggestions and criticisms were offered during the course of the study by C. W. Hibbard, University of Michigan, Dr. R. W. Wilson, University of Kansas and Dr. S. D. Durrant, University of Utah.

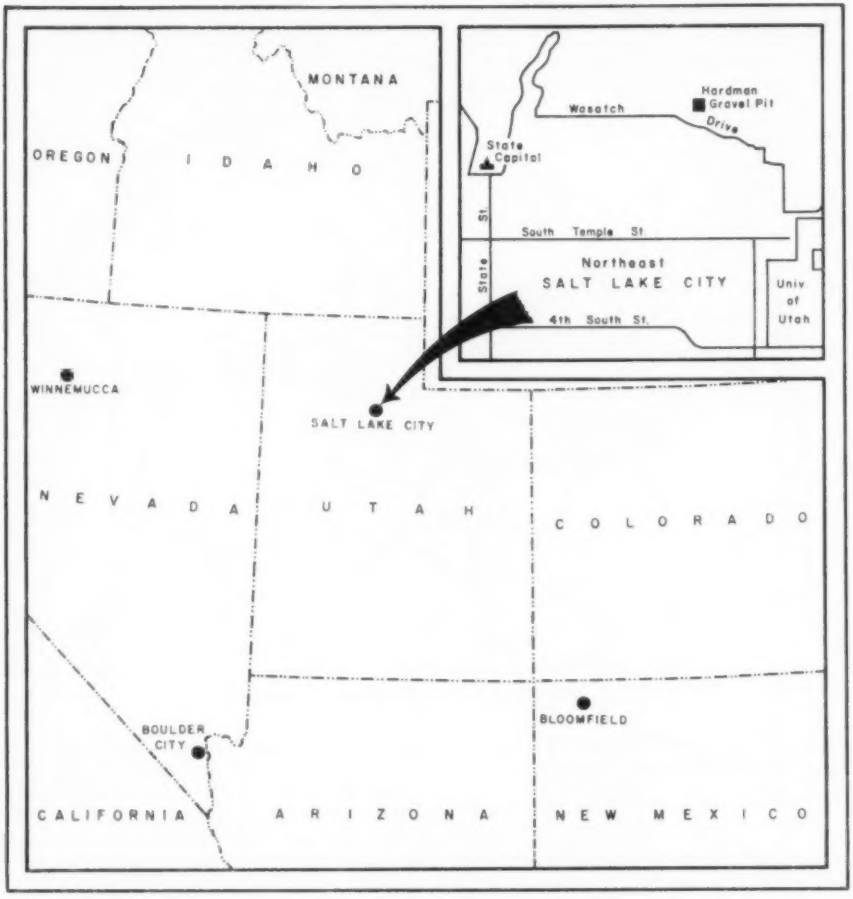
PREVIOUS CONTRIBUTIONS ON FOSSIL BIGHORN SHEEP FROM NORTH AMERICA

Very few papers have been published on Pleistocene bighorn sheep of North America. Among the significant reports are those of Osborn (1910) describing remains of *Ovis montana* from Washington Lake, Franklin Couty, Washington; of Lambe (1912) discussing remains from Pleistocene river gravels of Last Chance Creek in Yukon Territory; and of Frick (1937) of two bighorn sheep from the Kowak clay of Alaska. On the basis of skull and horn-cores Frick described a new species, *Ovis dorshi* and a new subspecies, *Ovis dalli kaiseni*.

More recently Stovall (1946) reported a partial skull with horn-cores from river gravels near Bloomfield, New Mexico. Stovall compared this specimen with modern species of *Ovis canadensis* and concluded that it belongs to the same species. Another important discovery is that reported by Hibbard and Wright (1956) from Catclaw Cave in Mohave County, Arizona. The find consists of a portion of the right lower jaw with five teeth (P_2 to M_3). This formed the basis for a new species, *Ovis catclawensis*, which is similar to the modern bighorn sheep of central Asia, *Ovis ammon*.

LIVING BIGHORN SHEEP

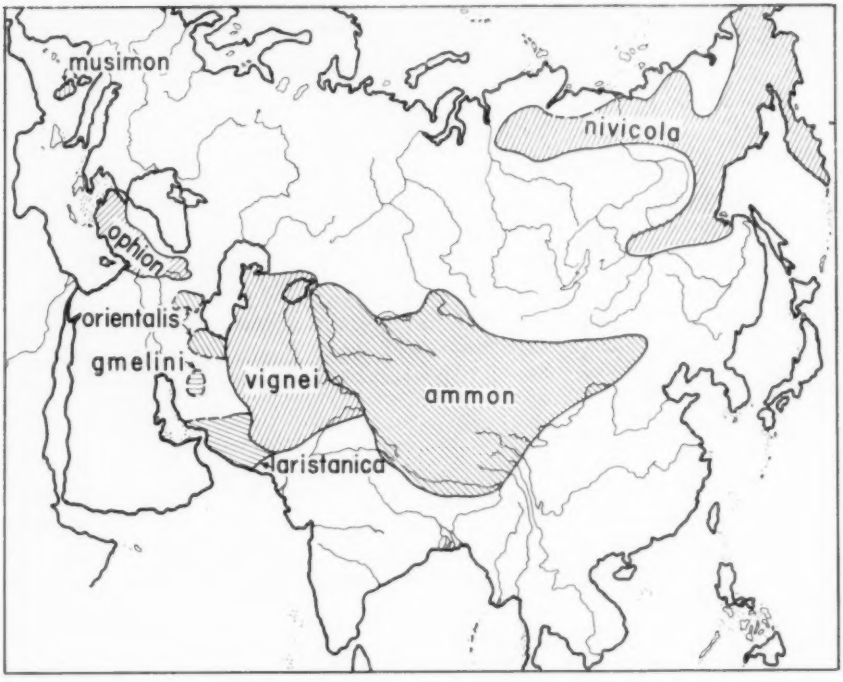
The bighorn is one of the few relatively large living mammals with which Pleistocene fossils may be compared. Eight species of bighorn sheep are found living in Eurasia; their approximate distributions are shown in text-figure 2. *Ovis musimon* is found only in Corsica and Sardinia; *Ovis ophion*, which apparently represents the ancestral stock of all bighorn sheep, is found only in Cyprus and southern Turkey; *Ovis orientalis*, *Ovis gmelini*, and *Ovis laristanica* have limited distributions in Iran and Pakistan; *Ovis vignei* is found mainly in Afghanistan and



TEXT-FIG. 1—Locality map showing sites where fossil bighorn sheep have been reported in the western interior of the United States.

the area immediately south of the Caspian Sea. *Ovis ammon*, found in Tibet, Mongolia, and southern Siberia, has the broadest distribution of any bighorn sheep in Eurasia; *Ovis nivicola* is found in the extreme northeastern part of Siberia. The first six species belong to the *Muflioniformes* which are much smaller sheep and apparently ancestral to the last two species, i.e., *ammon* and *nivicola* which belong to the *Argaliformes*.

There are only two species of bighorn sheep found in North America today—*Ovis dalli* and *Ovis canadensis*. There are two subspecies of *Ovis dalli*, both found in northwestern Canada and Alaska, while seven subspecies of *Ovis canadensis* are found in western North America. Text-figure 3 shows the distribution of North American species and subspecies prior to the sixteenth century. After this time extensive hunting has greatly reduced the number in North America. All of the North American bighorn sheep belong to the *Argaliformes* and were



TEXT-FIG. 2—Distribution of species of bighorn sheep in Eurasia.

apparently derived from the *ammon-nivicola* stock during Pleistocene times.

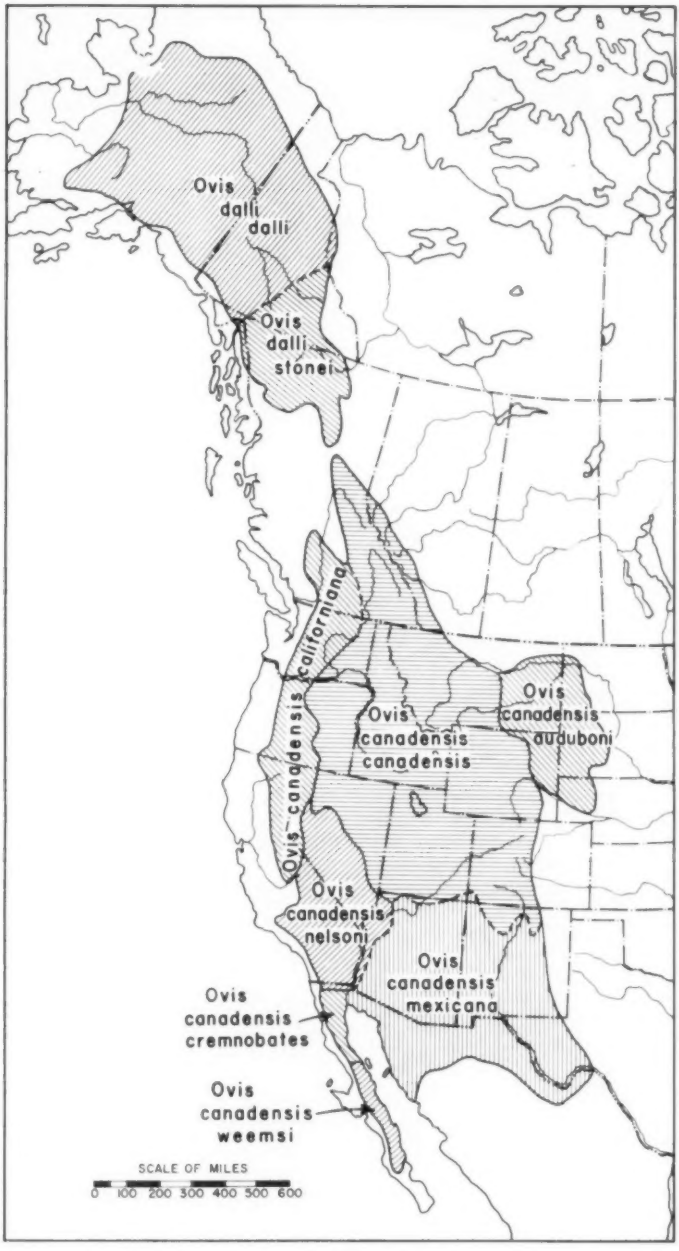
STRATIGRAPHIC AND ENVIRONMENTAL SIGNIFICANCE

All but one of the bighorn sheep specimens in the University of Utah collection are from the Pleistocene Alpine Formation. This formation is a deposit of the largest lake of the Bonneville basin and consists of gravel, sand, silt, and clay. At the present time, the age of the Alpine Formation is in doubt but studies currently in progress may serve to fix the age more or less accurately in terms of the standard Pleistocene subdivisions.

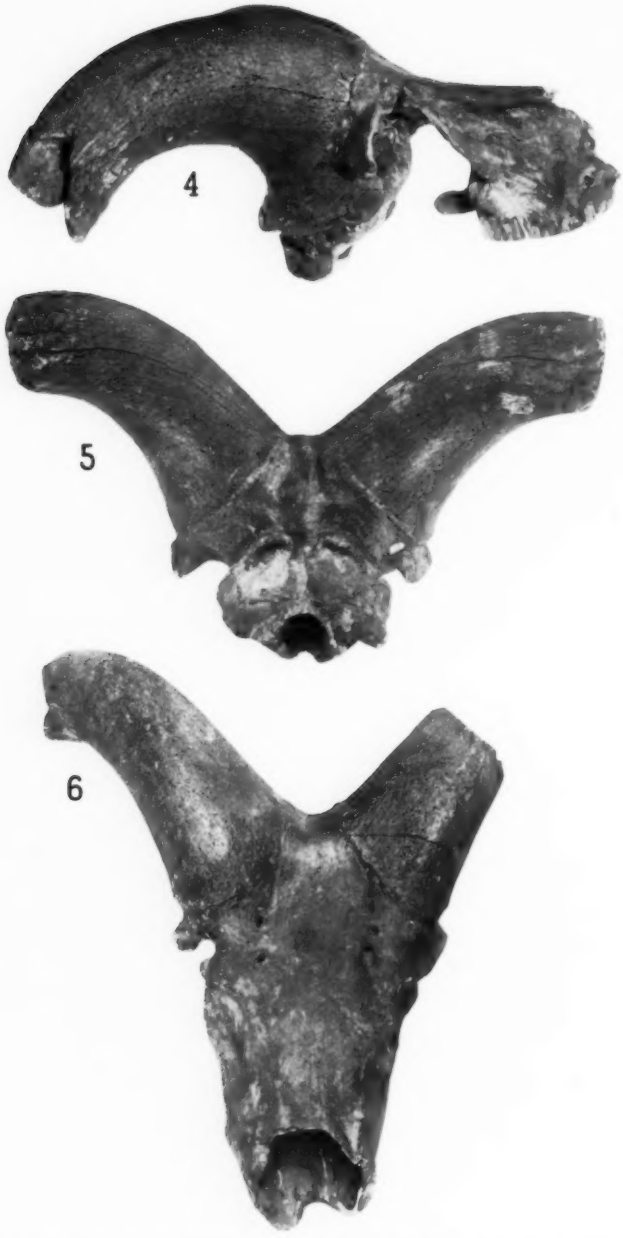
The bighorn remains are found in the nearshore facies of the Alpine Formation chiefly in gravel and coarse sand. The rapid burial by delta and embankment gravels from the steep shores of the lake are probably responsible for the preservation of the remains. Some of the bone fragments, however, show evidence of reworking by waves. The total absence of female or juvenile specimens and the scarcity of all but skulls with horn cores is difficult to explain. Perhaps the spot was frequented by solitary old males no longer associated with the herds in their more normal ranges. One important specimen was discovered beneath a volcanic ash bed in Willow Creek Canyon in northern Nevada. Apparently the individual was killed and buried by the Pleistocene ash fall.

SPECIMEN DESCRIPTIONS AND COMPARISONS

General Statement. Table 1 summarizes the horn core and skull measurements of fourteen of the Pleistocene specimens from the Great Basin, Stovall's Pleistocene *Ovis*, a modern *Ovis canadensis*, and a modern *Ovis ammon*. Table 2 includes what the authors believe to be the most significant of



TEXT-FIG. 3—Distribution of species and subspecies of bighorn sheep in North America before the sixteenth century.



TEXT-FIGS. *4–6*—*Ovis catclawensis* Hibbard and Wright. *4*, side view of cranium with horn cores and rostral elements attached; *5*, posterior view of another specimen from the same locality; *6*, face view of same specimen as Fig. *4*. Overall length of specimen *4* and *5*, 15½ inches.

TABLE 1—HORN CORE AND SKULL MEASUREMENTS OF THE GREAT BASIN SPECIMENS[1]

Specimen	Maximum diameter at base of horn cores	Minimum length of horn cores	Circumference of horn cores at base	Greatest distance between core tips	Minimum distance between horn core bases	Minimum angle between horn cores	Maximum orbital width	Maximum diameter of occipital condyles	Minimum mastoid width	Minimum basioccipital width	Minimum distance between inner edges of supraorbital foramina	Maximum width of skull at facial tuberosities	Maximum skull width at inner edge of infraorbital foramina
Bo 21	125	320	360	415	15	100°	180	72	113	32.5	63		
Bo 22	120	320	365		18						70		
Bo 23	126	355+	385					68	114	31			
Bo 24	124		357			105°					70		
Bo 25	108	297	330	388	28	90°	165	55	100	31	67		
Bo 26	126	342+	370		16	95°	165	67		29			
Bo 13	110		361										
Bo 5	117		363										
Bo 20	127	280+	380	370+	30	105°	184	75	115	33			
Bo 1	114		360										
Bo 2	101		317+										
Bo 40	116	305+	363		29	100°	166	83	109	32.5	63	106	61
Bo 41a	121		370		18		165	65	99	30			
ST-826	123	335+	380										
"O. canad." (Stovall, 1946)	118.5	317	346	413	28		173	63	103				
O. canad. (Dept. of Zool., Univ. of Utah)	120		335		16		162	68	103		73	99	57
O. ammon U.S. Nat. Museum	138	415	417		14	145°	180	81	126	40	80	105	60

[1] The New Mexico *"O. canadensis"* (Stovall, 1946), a modern *Ovis canadensis* from the Dept. of Zoology at the University of Utah, and a modern *Ovis ammon* from the U. S. National Museum are also tabulated for comparative purposes.

these measurements obtained from the Great Basin specimens; each measurement was made on no less than five individuals. Table 3 tabulates the jaw and teeth measurements of the Great Basin specimens along with two modern *Ovis canadensis*, modern *Ovis ammon*, and *Ovis catclawensis*. Table 4 summarizes and compares the most significant measurements obtained from the Great Basin specimens with the living North American subspecies of *Ovis canadensis* and *Ovis dalli* as determined by Cowan (1940). Text-figs. 4–6 show three views of the better Great Basin specimens.

Sexual, Age, and Individual Variations. Sexual variation affects bighorn sheep in essentially two ways: (1) the total size of the animal (males being the largest), and (2) the size and shape of the horns and horn cores. The males have much more massive horns and horn cores than do the females; the horns of the male are also longer and have a characteristic spiral shape, while the horns of the female are shorter, thinner, less curved, and more pointed. All of the Pleistocene Great Basin specimens are males as evidenced by the massive horn cores and large teeth.

TABLE 2—TABULATION OF THE MOST SIGNIFICANT MEASUREMENTS OBTAINED FROM THE GREAT BASIN BIGHORN SHEEP

	N*	M	R	SD
Maximum core circumference	12	363	330–385	14.1
Mastoid width	5	110	100–115	6.1
Minimum basioccipital width	6	32	29– 33	1.65
Orbital width	5	172	165–180	12.5
Maximum diameter of horn cores at base	12	118	101–127	6.7

* N = number of specimens; M = mean value; R = range of variation; SD = standard deviation.

TABLE 3—JAW AND TEETH MEASUREMENTS OF THE GREAT BASIN SPECIMENS COMPARED WITH OTHER BIGHORN SHEEP

Specimen	Palatine width at M3	Palatine width at P2	Alveolar length	Teeth measurements											
				Anterior-Posterior						Transverse width					
				P2	P3	P4	M1	M2	M3	P2	P3	P4	M1	M2	M3
Bo 40	61	38	100 upper	9	10	10	17.5	22	30	7.5	11	11.5	14	15	13.5
Bo 41b, c		39	93+ upper	8	9	9.5	18	22	28	8.5	10.5	12	14	14.5	14
Bo 42			lower					22	34				11.5	12.5	12
Ovis catclawensis (Hibbard & Wright, 1956)			101 lower								8.5	9.8	11	12.5	12.8
Ovis canadensis (Dept. of Zoology, University of Utah)	59	32	85 upper 86 lower	8 6	10 9	10 10.5	17 14	21 18.5	22 28	7.5 5.5	10 7	11 8	13 9.5	14 11	15 10.5
Ovis canadensis (Dept. of Anthropology, Univ. of Utah)			83 lower		7		12.5	17	27	6		8	10	10	
Ovis ammon (U. S. Nat. Museum)	60	40	100 upper	9.5	11	11	17	25	29	8	11	12	16	17	16

TABLE 4—COMPARISON OF COWAN'S MEASUREMENTS WITH THE GREAT BASIN SPECIMENS

Subspecies of *Ovis canadensis* and *Ovis dalli*	Mastoid width			Palatine breadth at M3			Palatine breadth at P2			Alveolar length			Minimum basioccipital width			Maximum core circumference		
	N[1]	M	R	N	M	R	N	M	R	N	M	R	N	M	R	N	M	R
canadensis	12	96	91–101	12	56	51–62	12	36	31–39	12	86	78–91	12	32	29–35	7	320	310–345
californiana	29	93	87– 98	29	57	54–62	29	35	31–41	29	88	81–94						
auduboni	2		89 and 92	2		58 and 59	2		32 and 34	2		92 and 94	2		28			
mexicana	3	87	84– 89	3	56	54–59	3	35	34–36	3	81	78–86						
nelsoni	11	90	85– 94	11	55	52–61	11	33	31–37	11	86	81–90						
cremnobates	6	88	87– 93	6	60	57–62	6	37	34–39	6	88	90–91						
weemsi	2		84 and 96	2		50 and 54	2		34 and 37	2		89 and 92						
dalli	18	89	84– 96	17	52	48–56	18	34	28–36	17	76	72–82						
stonei	12	90	82– 97	10	54	49–58	9	33	28–33	11	81	72–83						
Great Basin specimens	6	110	99–115	1		61	2		38 and 39	2		93[2] and 100	6	31.5	29–33	12	363	330–385

[1] N = number of specimens measured; M = mean value; R = range of variation.
[2] The measurement of 93 mm. obtained from Bo 41 represents a minimum value and may have been considerably larger.

The cranial sutures of the bighorn begin to fuse at about five years of age, and by the tenth year, all but the nasal-premaxillary sutures are completely fused. In most of the Great Basin specimens, sutures are difficult to trace with the naked eye, especially those between the frontal and parietal bones. The degree of fusion and the massiveness of the horn cores suggest that all specimens represent individuals ten years or more in age.

The modern specimens of *Ovis canadensis* and *Ovis dalli* described by Cowan (1940) as well as the modern specimens measured by the authors are also more than five years in age which insures a reliable comparative basis. Measurements of teeth are essential for species determination and comparison. Unfortunately, only three of the Great Basin specimens contain teeth.

Horn Core Measurements. The basal diameter and circumference of the horn cores were obtained from thirteen of the Great Basin specimens and represent maximum values. Apparently, these specimens lie between *Ovis ammon* and *Ovis canadensis* with respect to these two measurements. The range of variation of the basal circumference slightly overlaps that of *Ovis canadensis* (Tables 2 and 4).

Because the tips of the cores are missing in some of the specimens, the lengths of the cores (measured on the top side of the curve) represent minimum values. The distance between the horn core tips was available on only three specimens; this measurement also represents a minimum value. Because the tips are missing on most of the Great Basin specimens, these two measurements cannot be compared with the corresponding measurements on the horn cores of modern bighorns.

The minimum distance between the horn core bases apparently has little significance because of its wide range of variation in all of the specimens (15 to 30 mm.). The angle between the horn cores also represents a minimum value; this is the only horn core measurement in which there is a great difference between the Great Basin specimens and *Ovis ammon*.

Even though all of the Great Basin specimens are males of approximately the same age, there is an obvious wide range of variation. Individual variation in the horns of bighorn sheep lessens the value of horn core measurements in identification.

Skull measurements. Because the rim of the orbit is partially or completely missing in most specimens, the orbital width of the skull was taken with the calipers resting between the base of the horn core and the rim of the orbit. Cowan (1940) obtained the orbital width measurement between the notches on the rim of the orbit; for this reason, it is impossible to compare the two sets of data. The orbital width of two of the Great Basin specimens (Bo 21 and Bo 20) is very similar to the orbital width obtained from the modern *Ovis ammon;* this measurement taken from four other Great Basin specimens (Bo 25, Bo 26, Bo 40 and Bo 41a) is very close to the modern *Ovis canadensis*. The maximum diameter of the occipital condyles, because of its wide range of variation (55 to 83 mm.), apparently has little, if any, value.

The mastoid width (obtained from five of the Great Basin specimens) was taken with the calipers resting on the widest portion of the occiput. In some cases, parts of the occiput were missing and hence the results obtained are minimum values. This measurement is somewhat intermediate between *Ovis ammon* and *Ovis canadensis;* however, it most closely approaches that of *Ovis canadensis*.

The minimum width of the basioccipital was taken with the calipers resting on the inner edges of the foramina ovale; the values obtained for the distance between the supraorbital foramina were also taken with the calipers resting on the inner edges of the foramina. These two measurements are considerably greater in *Ovis ammon* than they are in the Great Basin specimens.

The width of the skull at both the facial tuberosities and the inner edges of the infraorbital foramina represent maximum values. Both of these measurements are almost identical to those obtained from the modern *Ovis ammon*.

Jaw and Teeth Measurements. Jaw and teeth measurements of three Great Basin specimens (Bo 40, 41, 42), *Ovis catclawensis*, two modern *Ovis canadensis*, and a modern *Ovis ammon* are summarized in Table 3.

The palatine width at M3 was taken with the calipers resting in the re-entrant notch;

while the palatine width at P2 was taken with the calipers resting between the maximum transverse widths of the premolars. There is very little difference between the palatine widths at M3 in any of the specimens measured (Pleistocene or modern). On the other hand, the palatine width at P2 obtained from the Great Basin specimens is much closer to that of *Ovis ammon* than it is to *Ovis canadensis*.

The alveolar length of the Great Basin specimens is almost identical to *Ovis ammon* and *Ovis catclawensis*, while it is from 15 to 18 mm. larger than the alveolar length obtained from the modern *Ovis canadensis*.

The anterior-posterior length of each of the upper pre-molars and molars of the Great Basin specimens is as great or greater than in the modern *Ovis canadensis*. Both the Great Basin specimens and *Ovis catclawensis* have a greater transverse width of each respective tooth (with exception of M3) than the transverse widths of either of the modern *Ovis canadensis*. In fact, with exception of the M2 and M3 measurements, the transverse widths are very close to those of *Ovis ammon*.

It is obvious from this table that most of the measurements obtained from the Great Basin specimens are much closer to corresponding measurements obtained from *Ovis ammon* and *Ovis catclawensis* than to those obtained from *Ovis canadensis*.

Comparisons with Cowan's data. Table 4 summarizes the comparative measurements of the Great Basin specimens and nine living North American subspecies of *Ovis canadensis* and *Ovis dalli*. The information pertaining to these living sheep is taken from Cowan (1940). Since no two individuals obtain measurements at exactly the same place minor differences in measurements are probably insignificant for classification purposes.

From column one of Table 4 it is apparent that the mastoid width of Great Basin sheep is greater than that of any living subspecies of bighorn sheep in North America with the exception of *O.c. canadensis;* the upper limits of the range of variation of *O.c. canadensis* overlaps only very slightly the lower limits of the range of variation of the Great Basin specimens. The maximum difference between the mean values of the mastoid width for the living bighorn sheep is 9 mm.; the minimum difference between the Great Basin bighorns and the living subspecies of North America is 14 mm. Apparently the mastoid width of the Great Basin sheep is much larger than any living species or subspecies of bighorn sheep in North America today.

Column two of Table 4 tabulates the data pertaining to the width of the palatine bone at the third molar. The one specimen in the Great Basin collection that this measurement could be obtained from showed it to fall within the upper limits of four subspecies of *Ovis canadensis*.

Column three of Table 4 compares the various widths of the palatine bone at the second premolar. Here again the Great Basin specimens fall within the upper limits of three living subspecies of *Ovis canadensis*.

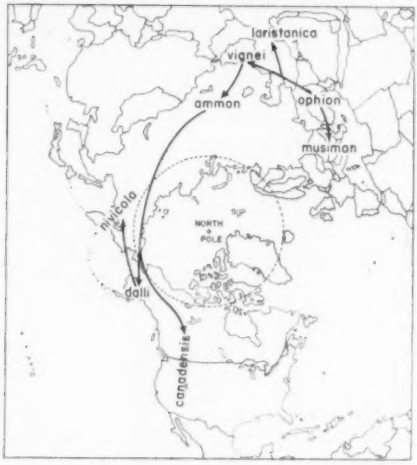
The alveolar length of the upper molar series of the Great Basin specimens is compared to the living North American forms in column 4. The two specimens that this measurement could be obtained from showed it to be greater than the range of variation for all but two subspecies (i.e., *o.c. auduboni* and *o.c. californiana*) of North American bighorn sheep.

The minimum basioccipital width of the Great Basin sheep falls well within the range of variation of the modern *O.c. canadensis* as shown in column 5. The range of variation of the maximum core circumference of modern *O.c. canadensis* overlaps 15 mm. with that of the Great Basin sheep as shown in column 6.

ORIGIN AND CLASSIFICATION OF NORTH AMERICAN PLEISTOCENE BIGHORN SHEEP

On the basis of comparative measurements it must be concluded that the Great Basin Pleistocene bighorn sheep do not belong to either of the two species now inhabiting North America. However, the jaw described by Hibbard and Wright (1956) apparently belongs to the same species as the Bonneville specimens and the specimen from Nevada. For this reason, the authors tentatively assign the Great Basin sheep to *Ovis catclawensis* after the holotype described by Hibbard and Wright.

The bighorn was one of the many animals that took part in a general migration across



TEXT-FIG. 7—Evolution-migration routes of bighorn sheep during Pleistocene time (after Shushkin, 1925).

the Bering Straits to North America during early Pleistocene times (Cowan, 1940). Ancestors of *Ovis catclawensis* apparently arrived in North America between the end of the Tertiary and the time of the Alpine Formation which is considered to be of early Wisconsin age.

The ancestry of North American bighorn sheep is not entirely clear. Cowan believes the reduced size of the rostral portions of the skull of *Ovis nivicola* is a primitive character and hence all American sheep had *nivicola*-like ancestors; he believes that *Ovis canadensis* (and *Ovis dalli*) are more recent and highly specialized forms of *Ovis nivicola*.

On the other hand, Sushkin (after Severtzov and Nassonov), 1925, believes the characters of *Ovis canadensis* are primitive and that those of *Ovis nivicola* (and *Ovis dalli*) are much more advanced. He states (p. 151):

> "Of the American and Siberian sheep which have many characters in common, *nivicola*, by its short ears and comparatively broad muzzle, differs more from other sheep; *canadensis*, by its lower ears and comparatively long and narrow muzzle, is considered as standing nearer to the High-Asian sheep, and probably in genetical connection with *ammon*."

Severtzov postulates a double migration theory to explain the origin of North American and Siberian sheep. He derives all bighorn sheep from the primitive stock, *Ovis ophion*, from the Aegean region of southern Europe. *Ovis ophion* apparently gave rise to (1) *Ovis musimon*, which migrated into southern Europe (2) *Ovis laristanica*, which migrated into southern Iran; and (3) *Ovis vignei* which migrated into northern Iran and Afghanistan region. *Ovis vignei*, in turn, gave rise to *Ovis ammon* (the first of the *Argaliformes*) which migrated into central Asia. Severtzov believes that the ancestors of *ammon* then migrated across the Bering Straits and gave rise to *canadensis* and *dalli*. Sometime during upper Pleistocene time, *dalli* ancestors migrated back across the Bering Straits giving rise to the most highly evolved of bighorn sheep, *Ovis nivicola*. Text-figure 7 shows the proposed evolution-migration routes suggested by Shushkin.

The Great Basin specimens apparently substantiate Severtzov's rather than Cowan's idea on the origin of North American bighorn sheep. Comparison between the Great Basin specimens and living specimens of *Ovis ammon*, *Ovis dalli*, and *Ovis canadensis*, indicate that the Great Basin sheep are much more closely related to the *ammon* stock than to the *canadensis* stock. It is believed that these specimens represent the *ammon*-like forms which migrated across the Bearing Straits in early or middle Pleistocene times. Through isolation (possibly caused by periodic ice sheets) these primitive forms evolved into *Ovis dalli* in northwestern North America and into *Ovis canadensis* in western and southwestern North America.

In summary, the following conclusions appear to be justified:

(1) The Pleistocene bighorn from the Great Basin do not belong to any living species.
(2) They are very similar to the extinct species, *Ovis catclawensis* (Hibbard and Wright, 1956), and for this reason they are tentatively assigned to this species.
(3) The Great Basin specimens are middle to late Pleistocene in age.
(4) They are more similar to the living species, Ovis *ammon*, which inhabits the High-Asian plateaus than they are to the living species *Ovis canadensis*, which inhabits western North America today. For this reason, it is believed that they represent a direct migration of *ammon*-like ancestors

to North America in middle Pleistocene times.

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MIOCENE FORAMINIFERA FROM THE LAJAS VALLEY, SOUTHWEST PUERTO RICO

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ABSTRACT—Fossils are recorded for the first time from a limestone in the Lajas Valley of southwest Puerto Rico. Twenty-three species of foraminifera are listed, and the other elements of the fauna are also recorded. Two foraminiferal species are new, *Pyrgo opima* and *Dendritina lajasensis*. It is concluded that the fauna is Miocene in age.

INTRODUCTION

THE LAJAS VALLEY of southwestern Puerto Rico is a broad, flat-bottomed valley infilled with alluvium and lacustrine deposits of Quaternary age. It is considered by Kaye (1957) to be a graben. The principal rocks of the area are mudstones, volcanics, and limestones, which belong to the Cretaceous and early Tertiary Older Series of Puerto Rico. In the valley itself, the occurrence of rocks belonging to the middle Tertiary Younger Series of Puerto Rico has been recorded by several authors including McGuiness (1948), Kaye (1957), and Matson (1960), but the age of these rocks has never been confirmed on the basis of fossil evidence. It is the purpose of the present paper to review such evidence as is available and to establish the age of these rocks as closely as possible.

In a survey of the Lajas Valley, useful fossils, principally foraminifera, were obtained from only one outcrop. This is an exposure of a crumbly light yellow chalky limestone, showing no bedding, which is seen in a low road cut between kilometer stones 17.8 and 17.9 on Puerto Rico highway 4. It is situated on the north side of the valley, just above the 25 meter contour and was recorded by Matson (1960) in his text as belonging to the Guanajibo formation. This formation was originally described by McGuiness (1948) from sub-surface occurrences in wells at Mayagüez, Puerto Rico, and other sub-surface limestones, sands, and clays in neighboring valleys of the western part of the island were placed with it by analogy. The Mayagüez material was said to be late Miocene or possibly Pliocene by Cushman on the basis of the foraminifera, although no report was published by him. None of the other occurrences of the Guanajibo formation have been dated paleontologically up to the present time, and the status of the formation as a stratigraphic unit is in some doubt.

[1] This paper is a contribution from the Institute of Caribbean Studies, Mayagüez, Puerto Rico.

FOSSILS OTHER THAN FORAMINIFERA

Apart from ostracodes, few fossils other than foraminifera were found in the Lajas Valley deposit. Among the microfossils were fish teeth, nepionic gastropods and pelecypods, fragments of crustacean pincers, and one spicule of an alcyonarian coral. Larger fossils included broken shells of several species of *Pecten* and internal casts of the following mollusks:

Natica sp.
Conus sp.
Cypraea sp.
Corbula sp.
Lucina sp.

Ostracodes were abundant and usually well preserved. Eight species were found:

Bairdia amygdaloides Brady
Buntonia sp.?
Costa meka van den Bold
Costa variabilicosta (van den Bold)
Cytherella aff. *sylverinica* Howe & Law
Cytherella sp.
Krithe aff. *producta* Brady
Perissocytheridea matsoni (Stephenson)

SYSTEMATIC DESCRIPTIONS OF THE FORAMINIFERA

Family VERNEUILINIDAE

Genus CLAVULINOIDES Cushman 1936

CLAVULINOIDES POLYGONALIS Galloway & Heminway

Clavulinoides polygonalis Galloway & Heminway, 1941, p. 327, pl. 7, figs. 4a,b.

Material.—One specimen.

Dimensions.—Length, 1.39 mm.

Remarks.—The only specimen which was found is not well preserved. It appears to belong to this species, which was described by Galloway and Heminway from the Aguada limestone (Quebradillas formation) between Río Piedras and Carolina, Puerto Rico. The Lajas Valley specimen is almost twice as long as the type specimen.

Family VALVULINIDAE
Genus CLAVULINA d'Orbigny 1826
CLAVULINA TRICARINATA d'Orbigny
Text-fig. 1—3,4

Clavulina tricarinata d'Orbigny, 1839, p. 111, pl. 2, figs. 16–18; Cushman, 1937, p. 22, pl. 3, figs. 1–3; Galloway & Heminway, 1941, p. 326, pl. 7, figs. 8a,b; Bermúdez, 1949, p. 79, pl. 4, figs. 11, 12.

Material.—7 specimens.

Dimensions.—Length, 0.8–1.41 mm.

Remarks.—d'Orbigny described this species from the Recent of Cuba and Jamaica. It is widely recorded from the West Indies as a living form, and it is known also from the Lower Oligocene of Alabama, the Middle Miocene Gurabo formation of the Dominican Republic, and the Miocene of Florida. It is regarded by Norton (1930) as being characteristic of "the shallow warm-water zone" and was found by him from the beach down to 16 fathoms. In northwestern Puerto Rico it ranges from the upper San Sebastián formation to the top of the Aymamon limestone; on the south coast it occurs in the Ponce limestone.

Genus VALVULAMMINA Cushman 1933
VALVULAMMINA CORNUCOPIA
Galloway & Heminway
Text-fig. 1—1,2

Valvulammina cornucopia Galloway & Heminway, 1941, p. 320, pl. 6, figs. 4a–c.

Material.—5 specimens.

Dimensions.—Height, 0.88–1.01 mm.

Remarks.—This species was described by Galloway & Heminway from the San Sebastián formation between Lares and San Sebastián, Puerto Rico. In northwestern Puerto Rico it ranges from the middle San Sebastián formation to the Aguada limestone; on the south coast it occurs in the Ponce limestone.

Family MILIOLIDAE
Genus QUINQUELOCULINA d'Orbigny 1826
QUINQUELOCULINA PYGMAEA Reuss
Text-fig. 1—18–20

Quinqueloculina pygmaea Reuss, 1850, p. 384, pl. 50, figs 3a–c; Galloway & Heminway, 1941, p. 304, pl. 2, figs. 7a–c.

Material.—2 specimens.

Dimensions.—Length, 0.61 and 0.73 mm.

Remarks.—The surface of the test is faintly striate when viewed with the light source at a low angle. Reuss described this species from the Miocene of Austria. In northwestern Puerto Rico it ranges from the middle San Sebastián formation to the Aguada limestone.

QUINQUELOCULINA LAMARCKIANA d'Orbigny
Text-fig. 1—5–7

Quinqueloculina lamarckiana d'Orbigny, 1839, p. 189, pl. 11, figs. 14,15.
Quinqueloculina vulgaris d'Orbigny; Galloway & Heminway, 1941, p. 305, pl. 2, figs. 6a–c.

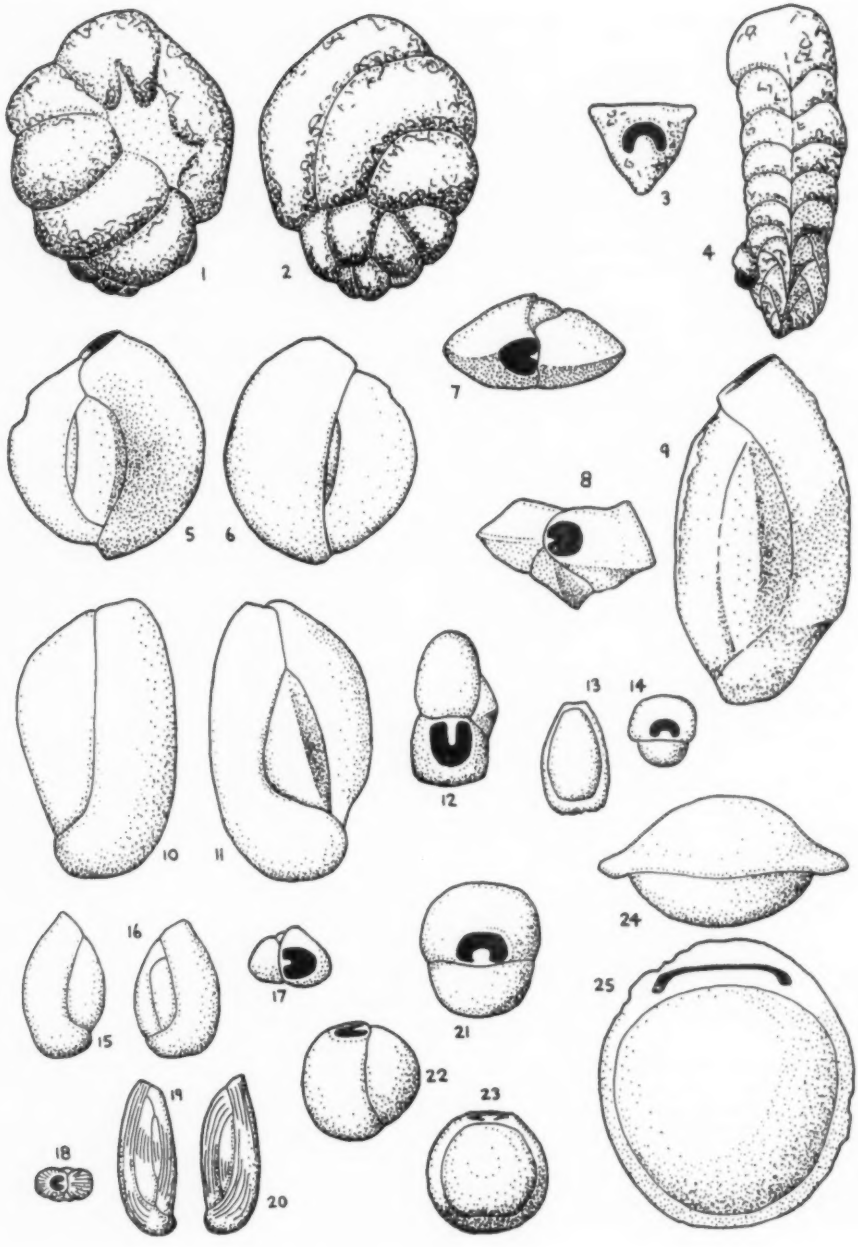
Material.—4 specimens.

Dimensions.—Widths of the specimens, 0.7, 0.72, 0.73, and 0.84 mm. The height is about one-eighth greater than the width in each case.

Remarks.—This species was described from the Recent of Cuba and Jamaica. It differs from *Q. vulgaris* d'Orbigny in being more angular at the periphery and in having a simple instead of a bifid tooth. Petters & Sarmiento (1956) record without illustration a form which they call *Quinqueloculina* cf. *lamarckiana* d'Orbigny from the Oligocene of Colombia, but with this possible exception the species does not seem to be known fossil outside Puerto Rico. In northwestern Puerto Rico it ranges from the middle San Sebastián formation to the Aguada limestone; on the south coast it occurs in the Ponce limestone. The Lajas Valley specimens differ slightly from the other Puerto Rican examples in not having the apertural lip which the latter usually display.

Genus SPIROLOCULINA d'Orbigny 1826
SPIROLOCULINA ANTILLARUM d'Orbigny
Text-fig. 1—8,9

Spiroloculina antillarum d'Orbigny, 1839, p. 166,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pl. 9, figs. 3,4; Galloway & Heminway, 1941, p. 300, pl. 1, figs. 6a–c.

Material.—One specimen.

Dimensions.—Height, 1.43 mm.

Remarks.—This species was described from the Recent of Cuba. In northwestern Puerto Rico it occurs in the lower Aymamon limestone; on the south coast it occurs in the Ponce limestone.

Genus TRILOCULINA d'Orbigny 1826
TRILOCULINA INFLATA d'Orbigny
Text-fig. 1—15–17

Triloculina inflata d'Orbigny, 1826, p. 300, no. 10; d'Orbigny, 1846, p. 278, pl. 17, figs. 13–15; Galloway & Heminway, 1941, p. 307, pl. 3, figs. 5a–c.

Material.—One specimen.

Dimensions.—Length, 0.57 mm.

Remarks.—The Lajas Valley specimen is not well preserved and is rather doubtfully ascribed to d'Orbigny's species, which was first described from the Recent, Mediterranean Sea, and fossil, from France and Italy. In 1846, d'Orbigny recorded it from the Miocene of Austria. In northwestern Puerto Rico it ranges from the middle San Sebastián formation to the Guajataca member of the Cibao marl formation; on the south coast it occurs in the Ponce limestone.

TRILOCULINA LAEVIGATA d'Orbigny
Text-fig. 1—10–12

Triloculina laevigata d'Orbigny, 1826, p. 300, no. 15; Galloway & Heminway, 1941, p. 308, pl. 3, figs. 6a–c.

Material.—3 specimens.

Dimensions.—Lengths, 0.64, 0.73, and 1.69 mm.

Remarks.—This species was described from the Recent, Mediterranean. In northwestern Puerto Rico it ranges from the upper San Sebastián formation to the Aguada limestone; on the south coast it occurs in the Ponce limestone.

Genus PYRGO Defrance 1824
PYRGO LUNULA (d'Orbigny)
Text-fig. 1—24,25

Biloculina lunula d'Orbigny, 1846, p. 264, pl. 15, figs. 22–24.

Pyrgo lunula (d'Orbigny); Galloway & Heminway, 1941, p. 311, pl. 4, figs. 4a–c.

Material.—6 specimens.

Dimensions.—Length, up to 1.33 mm.; usually between 0.8 and 1.2 mm.

Remarks.—This species was described by d'Orbigny from the Miocene of the Vienna basin. It is a large species, easily distinguished by its flat plate-like appearance. The aperture is indistinctly preserved in all the specimens from the Lajas Valley. In northwestern Puerto Rico it occurs from the upper San Sebastián formation to the middle Aymamon limestone; on the south coast it occurs in the Ponce limestone.

PYRGO OBLONGA (d'Orbigny)
Text-fig. 1—13,14

Biloculina oblonga d'Orbigny, 1839, p. 163, pl. 8, figs. 21–23.

Pyrgo oblonga (d'Orbigny); Galloway & Heminway, 1941, p. 312, pl. 4, figs. 5a–c.

Material.—2 specimens.

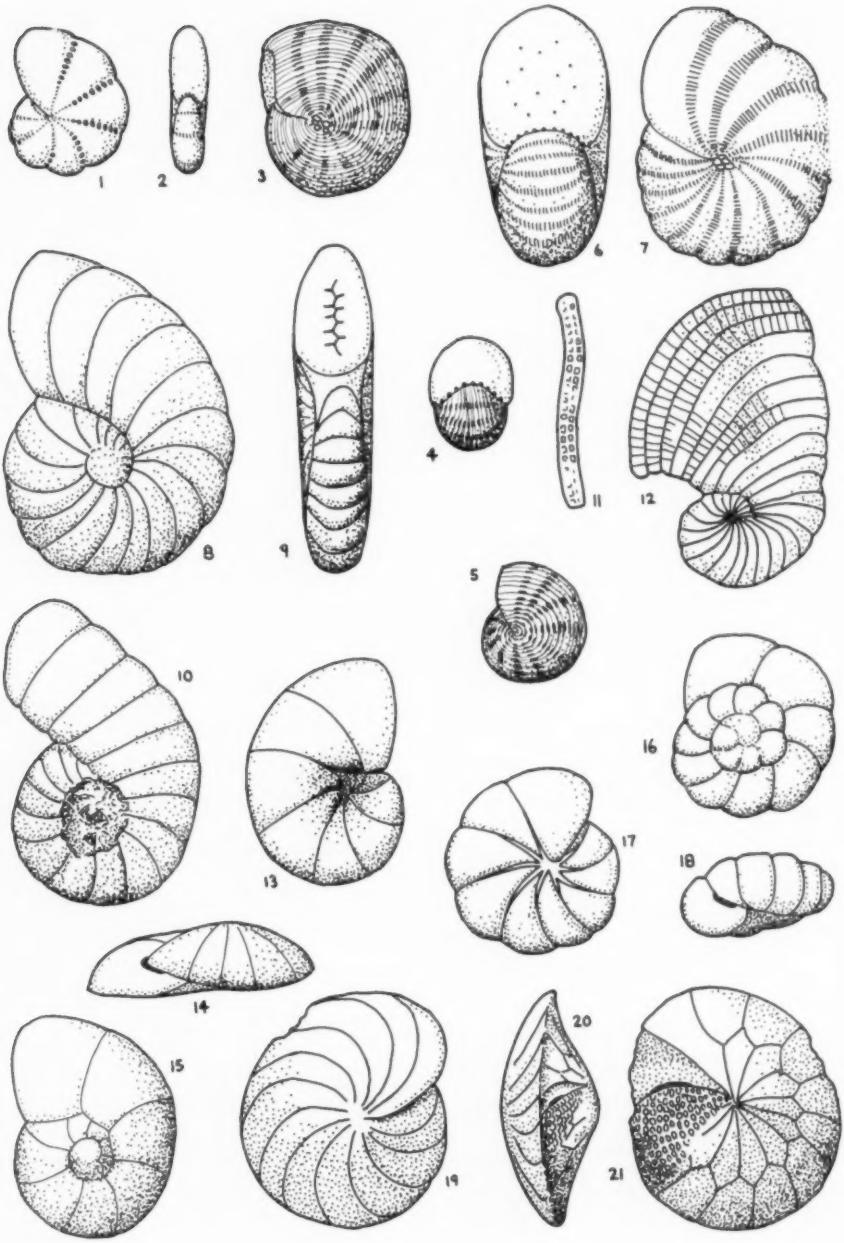
Dimensions.—Lengths, 0.37 and 0.42 mm.

Remarks.—This species was described by d'Orbigny from the Recent of Cuba. In northwestern Puerto Rico it ranges from the upper San Sebastián formation to the Aguada limestone; on the south coast it occurs in the Ponce limestone.

TEXT-FIG. *1*

(Figures ×36½, except 10–12 ×25, and 13, 14 ×48)

1,2—*Valvulammina cornucopia* Galloway & Heminway. *1*, apertural view. *2*, spiral view.
3,4—*Clavulina tricarinata* d'Orbigny. *3*, apertural view. *4*, side view.
5-7—*Quinqueloculina lamarckiana* d'Orbigny. *5,6*, side views. *7*, apertural view.
8,9—*Spiroloculina antillarum* d'Orbigny. *8*, apertural view. *9*, side view.
10–12—*Triloculina laevigata* d'Orbigny. *10,11*, side views. 12, apertural view.
13,14—*Pyrgo oblonga* (d'Orbigny). *13*, Front view. *14*, Apertural view.
15–17—*Triloculina inflata* d'Orbigny. *15,16*, Side views. *17*, Apertural view.
18–20—*Quinqueloculina pygmaea* Reuss. *18*, Apertural view. *19,20*, Side views.
21–23—*Pyrgo opima*, n. sp. Holotype. *21*, Apertural view. *22*, Side view. *23*, Front view.
24,25—*Pyrgo lunula* (d'Orbigny). *24*, Basal view. *25*, Front view.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PYRGO OPIMA, n. sp.
Text-fig. 1—21–23

Material.—6 specimens from the Lajas Valley, supplemented by 38 specimens from rocks of comparable age in northwestern Puerto Rico.

Description.—The test is smooth, globose; its length, width, and thickness are approximately equal to one another. The strongly inflated chambers are separated by a slightly depressed, smoothly curving suture. The aperture is large, elliptical, its length almost equal to half the width of the test. There is a broad apertural tooth which does not fill the aperture.

Dimensions.—Length, up to 0.8 mm.; usually about 0.6 mm.

Remarks.—*Pyrgo opima* may be distinguished from all other Puerto Rican species of *Pyrgo* by its globose form and large aperture. *Pyrgo peruviana* (d'Orbigny) is fairly similar, but it is more elongate than *P. opima*. In northwestern Puerto Rico, this species ranges from the middle San Sebastián formation to the Aguada limestone.

Family NONIONIDAE
Genus ELPHIDIUM Montfort 1808
ELPHIDIUM LOBATUM
Galloway & Heminway
Text-fig. 2—1,2

Elphidium lobatum Galloway & Heminway, 1941, p. 362, pl. 14, figs. 8a,b.

Material.—9 specimens.

Dimensions.—Greatest diameter, varies from 0.33 to 0.59 mm.

Remarks.—The Lajas Valley specimens are about twice the size of those of Galloway and Heminway which were described from the Lares limestone south of Arecibo, Puerto Rico. The aperture consists of a series of pores along the base of the last septal face, but it is not well preserved in any of my specimens.

ELPHIDIUM OWENIANUM (d'Orbigny)

Polystomella oweniana d'Orbigny, 1839, p. 30, pl. 3, figs. 3,4.

Elphidium owenianum (d'Orbigny); Galloway & Heminway, 1941, p. 363, pl. 14, figs. 9a,b; Becker & Dusenbury, 1958, p. 27, pl. 3, figs. 18a, b.

Material.—One specimen.

Dimensions.—Greatest diameter, 0.74 mm.

Remarks.—The Lajas Valley specimen is badly crushed, but there is no doubt that it belongs to this species, which was described by d'Orbigny from the Recent, coast of Patagonia. It is also known from the Aquitanian of Colombia. In northwestern Puerto Rico it occurs from the lower San Sebastián formation to the upper Cibao marl formation; on the south coast it occurs in the Ponce limestone.

ELPHIDIUM PUERTORICENSE
Galloway & Heminway
Text-fig. 2—6,7

Elphidium puertoricense Galloway & Heminway, 1941, p. 364, pl. 15, figs. 2a,b; Bermúdez, 1949, p. 171, pl. 11, fig. 24.

Material.—20 specimens.

Dimensions.—Greatest diameter, 0.97 mm. in the largest specimen; usually about 0.7 mm.

Remarks.—This species was described by Galloway and Heminway from the San

←

TEXT-FIG. 2

(Figures ×36½, except 1,2,13–18, ×48 and 19–12 ×25)

1,2—Elphidium lobatum Galloway & Heminway. *1*, Side view. *2*, Apertural view.
3,4,5—Elphidium sagrai (d'Orbigny) subsp. *percrassum* Galloway & Heminway. *3,5*, side views. *4*, apertural view.
6,7—Elphidium puertoricense Galloway & Heminway. *6*, apertural view. *7*, side view.
8,9,10—Dendritina lajasensis, n. sp. *8*, side view of holotype. *9*, apertural view of holotype. *10*, side view of paratype.
11,12—Archaias aduncus (Fichtel & Moll). *11*, edge view. *12*, side view.
13–15—Cibicides americanus (Cushman). *13*, umbilical view. *14*, apertural view. *15*, spiral view.
16–18—Rotalia beccarii (Linné) subsp. *parkinsoniana* (d'Orbigny). *16*, spiral view. *17*, umbilical view, *18*, apertural view.
19–21—Amphistegina floridana Cushman & Ponton. *19*, dorsal view. *20*, apertural view. *21*, ventral view.

Sebastián formation, near Collazo Falls, Puerto Rico. It also occurs in the Lower Miocene Arroyo Blanco formation of the Dominican Republic. The Lajas Valley specimens are slightly larger than the type, but otherwise they are very similar. In northwestern Puerto Rico this species ranges from the middle of the San Sebastián formation to the lower Aymamon limestone; on the south coast it occurs in the Ponce limestone.

ELPHIDIUM SAGRAI (d'Orbigny) subsp. PERCRASSUM Galloway & Heminway
Text-fig. 2—3–5

Elphidium sagrai crassum Galloway & Heminway, 1941, p. 366, pl. 15, figs. 1a,b.
Elphidium sagrai (d'Orbigny) subsp. *percrassum* Galloway & Heminway; Thalmann, 1951, p. 222.

Material.—24 specimens.

Dimensions.—Greatest diameter, 0.72 mm. in the largest specimen; usually about 0.5 mm.

Remarks.—Galloway & Heminway described this form from the San Sebastián formation, near Collazo Falls, Puerto Rico. The subspecies differs from the species of d'Orbigny in having more elongate sutural depressions and a more lunate apertural face. In northwestern Puerto Rico it ranges from the middle San Sebastián formation to the Guajataca member of the Cibao marl formation; on the south coast it occurs in the Ponce limestone.

Family PENEROPLIDAE
Genus DENDRITINA d'Orbigny 1826
DENDRITINA LAJASENSIS, n. sp.
Text-fig. 2—8–10

Material.—34 specimens.

Description.—The test is smooth, compressed, umbilicate, planispirally coiled, involute at first but becoming evolute or uncoiled later. There are 13–15 chambers in the last whorl. The sutures are limbate, depressed, and the margin of the test is lobulate. The aperture is narrow, elongate, dendritic, in the middle of the apertural face.

Dimensions.—Greatest diameter, 1.34 mm. in the largest specimen; usually about 0.8–1.0 mm.

Remarks.—This species is about the same size as the only other *Dendritina* recorded from Puerto Rico, *D. preëlegans* Galloway and Heminway, but it differs from the older species in having no ornament, having more chambers in the last whorl, and in its narrower aperture. *D. lajasensis* is the most common species in the Lajas Valley fauna, but it is not at present known from elsewhere in Puerto Rico.

Genus ARCHAIAS Montfort 1808
ARCHAIAS ADUNCUS (Fichtel & Moll)
Text-fig. 2—11,12

Nautilus aduncus Fichtel & Moll, 1798 (1803 reprint), p. 115, pl. 23, figs. a–e.
Archaias aduncus (Fichtel & Moll); Galloway & Heminway, 1941, p. 317, pl. 5, figs. 8a–c.

Material.—11 specimens.

Dimensions.—Diameter, 0.9–2.2 mm.; usually about 1.8 mm.

Remarks.—This species was first described from the Recent, Arabian Sea. In northwestern Puerto Rico it ranges from the lower Lares limestone to the lower Aymamon limestone; on the south coast it occurs in the Ponce limestone.

ARCHAIAS COMPRESSUS (d'Orbigny)

Orbiculina compressa d'Orbigny, 1839, p. 66, pl. 8, figs. 4–7; Cushman, 1919, p. 70, pl. 7, fig. 6.
Archaias compressus (d'Orbigny); Galloway & Heminway, 1941, p. 318, pl. 5, figs. 10a,b; Cole, 1957, p. 328, pl. 24, figs. 1–9.

Material.—10 specimens.

Dimensions.—Greatest diameter, 0.98 mm. on the largest specimen; usually about 0.8 mm.

Remarks.—This species was first described from the Recent, West Indies, but it ranges back at least to the Upper Oligocene Bohio and Caimito formations of the Panama Canal Zone (Cole, 1957). In northwestern Puerto Rico it occurs from the middle San Sebastián formation to the Aguada limestone; on the south coast it occurs in the Ponce limestone.

Family ROTALIIDAE
Genus DISCORBIS Lamarck 1804
DISCORBIS FLORIDANA Cushman

Discorbis floridana Cushman, 1922, p. 39, pl. 5, figs. 11, 12; Bermúdez, 1949, p. 238, pl. 15, figs. 16–18.

Material.—One specimen.

Dimensions.—Greatest diameter, 0.37 mm.

Remarks.—Cushman described this species from the Recent of Florida, and it has been recorded by Bermúdez from the Upper Miocene Las Salinas formation of the Dominican Republic. The Lajas Valley specimen referred to *D. floridana* is not well preserved, but in northwestern Puerto Rico this species ranges from the upper San Sebastián formation to the Aguada limestone.

DISCORBIS OLIGOSPIRATUS
Galloway & Heminway

Discorbis oligospiratus Galloway & Heminway, 1941, p. 384, pl. 21, figs. 1a–c.

Material.—2 specimens.

Dimensions.—Greatest diameter of the specimens, 0.71 and 0.9 mm.

Remarks.—The Lajas Valley specimens agree well with the type of the species, which was described from the Cibao marl formation between Manatí and Ciales, Puerto Rico.

Genus ROTALIA Lamarck 1804
ROTALIA BECCARII (Linné) subsp.
PARKINSONIANA (d'Orbigny)
Text-fig. 2—16–18

Rosalina parkinsoniana d'Orbigny, 1839, p. 99, pl. 4, figs. 25–27.
Streblus beccarii (Linné) var. *parkinsoniana* (d'Orbigny); Bermúdez, 1949, p. 233, pl. 15, figs. 43–45.

Material.—One specimen.

Dimensions.—Greatest diameter, 0.61 mm.

Remarks.—This form was described by d'Orbigny from the Recent of Cuba and Europe. Bermúdez records it from the Middle Miocene Arroyo Seco formation of the Dominican Republic. In northwestern Puerto Rico it occurs from the upper San Sebastián formation to the Aguada limestone. The Puerto Rican specimens are variable, some lacking the covering of clear shell material over the inner whorls but others being identical with the specimens from the Dominican Republic.

Family AMPHISTEGINIDAE
Genus AMPHISTEGINA d'Orbigny 1826
AMPHISTEGINA FLORIDANA
Cushman & Ponton
Text-fig. 2—19–21

Amphistegina floridana Cushman & Ponton, 1932, p. 96, pl. 14, figs. 6,7; Galloway & Heminway, 1941, p. 408, pl. 28, figs. 5a–c; Bermúdez, 1949, p. 263, pl. 19, figs. 4–9.
aff. *Amphistegina chipolensis* Cushman & Ponton, 1932, p. 96, pl. 15, figs. 1a–c.
aff. *Astigerina choctawensis* Cushman & McGlamery, 1938, p. 111, pl. 28, figs. 2a–c.

Material.—28 specimens.

Dimensions.—Greatest diameter, 2.1 mm. on the largest specimen; usually between 0.8 and 1.3 mm.

Remarks.—This species was described by Cushman and Ponton from the Lower and Middle Miocene of Florida. The differences between the type of *Amphistegina floridana* and the types of *Amphistegina chipolensis*, from the Lower Miocene of Florida, and *Asterigerina choctawensis*, from the Middle Oligocene Byram marl of Alabama, do not seem to be very great. Probably, these three forms are closely related chronologic subspecies on a continuous evolutionary series. Cushman and Ponton (1932) have already suggested that *A. chipolensis* is ancestral to *A. floridana*.

In northwestern Puerto Rico, *A. floridana* ranges from the middle San Sebastián formation to the top of the Aymamon limestone. On the south coast it occurs in the Ponce limestone.

Family ANOMALINIDAE
Genus CIBICIDES Montfort 1808
CIBICIDES AMERICANUS (Cushman)
Text-fig. 2—13–15

Truncatulina americana Cushman, 1918, p. 63, pl. 20, figs. 2–3; pl. 21, fig. 1.
Cibicides americanus (Cushman); Galloway & Heminway, 1941, p. 390, pl. 24, figs. 3a–c.

Material.—One specimen.

Dimensions.—Greatest diameter, 0.73 mm.

Remarks.—This species was first described from the Miocene Duplin marl of South Carolina. In northwestern Puerto Rico it occurs from the upper San Sebastián formation to the lower Cibao marl formation.

SIGNIFICANCE OF THE FORAMINIFERA

Twenty-three species of foraminifera occur in the Lajas Valley deposit. The composition of the foraminiferal fauna is tabulated below:

Family	No. species	No. species expressed as percentage of total no. species	No. specimens expressed as percentage of total no. specimens
Verneuilinidae	1	4	2
Valvulinidae	2	9	7
Miliolidae	8	35	13
Nonionidae	4	17	34
Peneroplidae	3	13	20
Rotaliidae	3	13	3
Amphisteginidae	1	4	15
Anomalinidae	1	4	6

Comparison of this fauna with the faunas described by Norton (1930) from the Recent seas, principally of Florida and the West Indies region, shows that the Puerto Rican material corresponds well with Norton's "zone A." This is the zone from the beach down to five fathoms, with a temperature range of 21.5–31.4°C. The Lajas Valley fauna differs from it in having a much smaller proportion of Miliolid specimens, but the other elements of the fauna correspond closely. The Lajas Valley assemblage is therefore considered to be a shallow water fauna, a conclusion which is supported by the general nature of the macrofossils and by the complete absence of planktonic foraminifera.

Correlation of the deposit.—The foraminifera are more closely related to those of northwestern Puerto Rico than to the geographically closer south coast outcrops of middle Tertiary beds. Twenty-two of the twenty-three Lajas Valley species are known to occur also in northwestern Puerto Rico, but only thirteen are as yet known from the southern outcrops of middle Tertiary rocks. Comparison can therefore best be made with the middle Tertiary of the northwest of the island. The succession there has been divided by Zapp, Bergquist, & Thomas (1948) as follows:

Aymamon limestone
Aguada limestone
Cibao marl, including the Guajataca member
Lares limestone
San Sebastián formation

The three lower formations are in part facies of each other. This middle Tertiary sequence has been considered by several authors to be broadly Middle Oligocene to Lower Miocene (Meyerhoff, 1933; Woodring, 1943; Zapp *et al.*, 1948), but Gordon (1960) suggested that it is Lower and Middle Miocene.

The Lajas Valley fauna is most similar to that of the topmost San Sebastián formation, in which sixteen of the Lajas Valley species are also present, and to that of the Lares limestone, in which there are eighteen of the Lajas Valley species. However, this correlation is at least as likely to be one of like facies as it is to be one of age since the topmost San Sebastián formation and the Lares limestone are thought by the writer to have accumulated in water equally as shallow as that in which the Lajas Valley deposit was formed. Unfortunately, the Lajas Valley foraminifera include no good marker species, and in the absence of these no close correlation can be made. On the other hand, the fauna is Miocene in general composition, and comparison with other described faunas of the Caribbean region suggests that it may not be older than Middle Miocene. This conclusion is supported by the ostracodes of the deposit, which indicate a Miocene age when compared with the faunas described from Trinidad by van den Bold (1957, 1958, 1960). The poorly preserved macrofossils provide no supplementary evidence as to the age of the deposit.

Acknowledgment.—The author wishes to record his thanks to Dr. J. D. Weaver, Professor of Geology at the Mayagüez campus of the University of Puerto Rico, for his interest and encouragement during the course of the work.

Depository of fossils.—Holotypes of the new species and other representative specimens will be presented to the United States National Museum.

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JOURNAL OF PALEONTOLOGY, V. 35, NO. 3, P. 620–624, 1 TEXT-FIG., MAY, 1961

THE SUPPOSED PLIOCENE PEBAS BEDS OF THE UPPER JURUÁ RIVER, BRAZIL

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ABSTRACT—Berry and Maury described plants and mollusks believed by them to come from an extension of the Pliocene Pebas formation from Peru into the Brazilian Territory of Acre. The correlation is entirely unjustified. Certainly some and probably all of the fossils in question are from latest Pleistocene or, most likely, fully Holocene oxbow fillings, and not from any widespread formation or of any earlier age.

INTRODUCTION

In 1935 and 1936 Pedro de Moura and Alberto Wanderley collected freshwater pelecypods and leaves in clays from the Upper Juruá and its tributaries in the Territory of Acre, Brazil. These were submitted through the Serviço Geológico do Brasil to Carlotta J. Maury, who in turn sent the leaves to Edward W. Berry for identification. Both Maury and Berry published on the collection, in a curiously uncoordinated way as will be further mentioned. Berry (1937) concluded that if the beds "are as old as the Pliocene, they should probably be regarded as late Pliocene in age." He made no unequivocal correlation, but compared the leaf-bearing beds of the Upper Juruá with the Pebas formation of Peru (see Gardner, 1927) and spoke of the "great lateral extent" of similar beds along or near the Marañón and Ucuyali in Peru, the Napo in Ecuador, and now the Juruá in Brazil. Maury (1937) considered the Upper Juruá deposit as definitely Pliocene and stressed explicit correlation with the Pebas beds. On that excellent authority, the expansion into Acre of the Pebas beds (or equivalent) and of a corresponding freshwater, brackish, or perhaps even marine Pliocene embayment has become generally accepted. It is, for instance, given as factual and without question in Oliveira & Leonardos (1943) and in Jenks (1956), the standard reference volumes for Brazilian geology. That is, nevertheless, certainly incorrect, on evidence here to be presented.

The limited but crucial field observations involved in the present note were made by a joint Brazilian-American expedition sponsored by the Instituto Nacional de Pesquisas da Amazônia with the collaboration of the American Museum of Natural History (New York), the Museu Paraense Emílio Goeldi (Belem), and the Departamento Nacional de Produção Mineral (Rio de Janeiro). North American participation was supported in part by a grant from the National Science Foundation. Dr. L. I. Price led the party on behalf of the cooperating Brazilian institutions. More complete details and acknowledgements will be published with fuller reports of the results. The present note treats a point of considerable importance, but one only incidental to the main purposes and accomplishments of the expedition.

PLANTS

Berry returned the fossil plants to Maury with identifications of three previously known species and the notation that four species were new. Maury (1937) published Berry's identifications and applied names to the species indicated as new by Berry. In the meantime Berry was unaware of Maury's intention to publish and he also proceeded to publish on the collection, giving another set of names to the supposedly new species (Berry, 1937). He raised their number to six, changed two of the generic references he had given to Maury, and added an identification not given to (or at least not published by) Maury. Maury's descriptions are not worded like Berry's and are slightly contradictory on one or two points. It is, however, clear that the same specimens are being described, that Maury depended on Berry's authority for their identification, and that the pairs of specific names given independently by Berry and Maury are objective synonyms. Both papers were published in 1937 and I can find

no evidence as to which was earlier, but priortiy is not important as it is improbable that the species are valid in any case.

The floral lists of Berry and of Maury are as follows, with identical forms alined:

Berry, 1937	Maury, 1937
1. *Coussapoa* sp.	*Coussapoa* sp.
2. *Cassia aguaytiensis* Berry, 1925.	*C. aguaytiensis.*
3. *Machaerium premuticum* Berry, 1937.*	*M. acreanum* Maury, 1937.*
4. *Vochysia acuminatafolia* Hollick and Berry, 1924	*V. acuminatafolia.*
5. *Sapium* (?) *pliocenicum* Berry, 1937.*	*Omalanthus* or *Sapium* sp.
6. *Sparattanthelium pliocenicum* Berry, 1937.*	[Not included]
7. *Mespilodaphne acrensis* Berry, 1937.*	*M. wanderleyi* Maury, 1937.*
8. *Persea amoneana* Berry, 1937.*	*P. euzeboi* Maury, 1937.*
9. *Bignonites mauryae* Berry, 1937.*	*Banisteria demouroi* Maury, 1937.*
10. *Endlichera rhamnoides* Engelhardt, 1895.	*E. rhamnoides.*

The starred names are those considered new species by these authors in 1937. The numbers were not used by Berry or Maury but are introduced here for reference to the discussion below.

Maury briefly described specimens of each form recognized by her after Berry's notes, but she made no explicit specific comparisons or diagnoses. She merely accepted Berry's authority that the species were new. All the listed species are supposedly extinct, which would certainly seem to indicate considerable geological age. But the evidence is valueless, as the following annotations show:

1. Not identified beyond the genus, which "contains about a score of existing [i.e., Recent] species" (Berry, 1937).

2. Species originally named from fossils from the Rio Aguaytia in Peru. Berry (1925) noted that many species of *Cassia* "both fossil and recent are practically indistinguishable from the present species, so that extended comparisons would be without significance," and no comparisons at all were given. This extraordinary statement seems to imply that if a specimen is not in fact distinguishable from numerous known species it may still properly be referred to a "new" species and comparisons may then be considered superfluous! The age of the Aguaytia flora is unknown. Berry said that it could be of any age in the Tertiary, and he gave no convincing evidence that it is not post-Tertiary. Since the Aguaytia "species" was not really defined or distinguished, the reference to it of Juruá specimens would have no correlational value in any case.

3. "Very close to the existing Brazilian species *Machaerium muticum* . . . It differs from the recent form in its more curved and more ascending secondaries" (Berry, 1937).

4. The species was originally described from Marahii, Brazil. Hollick and Berry (1924) gave no differential diagnosis and said that the supposedly extinct form is practically identical with a Recent species. The age of the Marahii specimen was said to be Pliocene, but Hollick and Berry made it clear that the age was not really determined.

5. "The material is too incomplete for accurate determination" and comparisons with Recent species "common in the bottom lands of the Amazon systems" (Berry, 1937) were not made.

6. Said by Berry (1937) to be "practically indistinguishable" from a Recent species, and no distinction was given.

7. "Not unlike a number of existing species in the same general region" (Berry, 1937) with which no comparison was made.

8. "Comparable with a number of existing species of the same general region" (Berry, 1937) and again not compared with them.

9. *Bignonites* is a "form genus" and the fossil is not identifiable to genus. It is "close to existing species in the same general region" (Berry, 1937) and was not distinguished from them.

10. The supposed species was described by Engelhardt (1895) from specimens of unknown age from Loja, Ecuador. Engelhardt noted resemblance to a Recent species and did not give a differential diagnosis. Berry (1937) felt doubts as to the generic ascription. Neither author made adequate comparisons with the many similar Recent species from the same regions.

Thus of the ten supposedly extinct spe-

cies, nine have not been distinguished in any way from Recent species. The only one for which a diagnosis was really given, *Machacrium premuticum*, was distinguished by characters so trifling that the possibility of mere individual variation must be considered. Moreover, it is most improbable that specimens of *Machaerium* now living along the Juruá were available for comparison. No real reason has been adduced for considering this "fossil flora" as anything but a small sampling of the strictly Recent flora of the same locality. The conclusion is inescapable that Berry merely assumed that the species were extinct because the leaves had been buried, something that happens every year to innumerable Recent leaves in identical circumstances.

MOLLUSKS

Moura & Wanderley collected pelecypods from Porto Peter on the Juruá, the same locality as for most of Berry's Juruá plants, and also from the Jesumira, a small tributary of the Môa, which in turn flows into the Juruá just above Cruzeiro do Sul. Maury (1937) published on these specimens, placing some from both localities in a supposedly new species *Anisothyris acreana* and referring some from the Jesumira to *Anisothyris* cf. *ovata* Conrad.

Anisothyris Conrad (= *Pachydon* Gabb) is a supposedly extinct genus of pelecypods common in the Pebas beds of Peru, from which several species have been named. It is defined by hinge characters and by unequal valves with prominent beaks, at least one of which is strongly spiral. Maury's specimens from the Juruá were poorly preserved as molds in soft clay. Beaks are present but are not particularly prominent and are not spiral. Maury speaks of the Juruá species as "slightly inequivalve," but her figure shows absolutely symmetrical valves. The hinge structure is "not clearly enough shown for illustration, but traces of hinge structure indicate that the shell is referable to the genus *Anisothyris*" (Maury, 1937).

Dr. Dwight W. Taylor of the U. S. Geological Survey (personal communication) has commented as follows on Maury's identifications of these mollusks:

"Despite the fact that these internal molds do not retain the hinge characters well, the roughly circular outline and equivalve condition which they do show are adequate to indicate that they do not belong to *Pachydon* (= *Anisothyris*) or to the Corbulidae. The size, shape, and thinness of the shell suggest the family Corbiculidae, of fresh and brackish-water habitats, perhaps the genus *Polymesoda*. Recent mollusks of the Amazon Basin are not well known, and I cannot refer the supposed *Pachydon* definitely to species living locally. The correlation with the Pebas beds is unwarranted."

The supposed paleontological evidence of Pliocene age or of correlation with the Pebas is thus completely worthless. As far as the evidence either of the plants or of the mollusks goes, the deposits could be Recent.

FIELD OBSERVATIONS

Our 1956 expedition visited the crucial locality, source of most of the fossils described by Berry and by Maury, designated by Maury as "Montante Porto Peter," evidently from Moura's field data. The locality is on the right bank of the Alto Juruá immediately above Porto Peter, which in spite of its pretentious name consists of a single rubber gatherer's hut. The deposit is largely semiplastic carbonaceous clay, partly banded or varved. In addition to a few poor impressions of pelecypods, it contains numerous leaves, some almost fresh, some carbonized, and some (as noted by Berry for specimens seen by him) partly replaced by vivianite. The differences in preservation are not correlated with depth in the deposit or, consequently, with age.

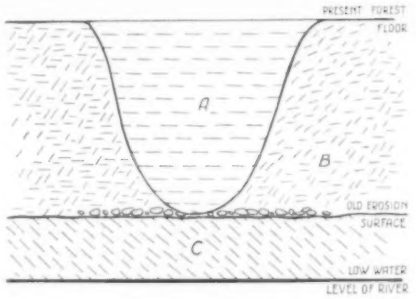
These leaf-bearing clays are the filling of a former oxbow lake, and their exposure in the present river bank is due to transverse cutting by a later cycle of meandering. The Alto Juruá and its main tributaries meander extensively. All stages from formation of a new oxbow through its filling with sediment and subsequent cutting by later meandering can be observed at numerous places along those streams. The process of burial of leaves and other debris in the oxbow sediments can also be observed going on at the present time. Each of these deposits is a separate "stratigraphic unit" or diminutive "basin filling" on its own account, from a few hundred meters up to a kilometer or so in longest dimension. They obviously do not

constitute a formation in the usual sense of the word or a widespread single lake or embayment deposit such as was evidently envisioned by Berry, Maury, and others following them. Although the various oxbow fillings clearly are not precisely contemporaneous, none seen by us can be older than latest Pleistocene and most, perhaps all in this area, are geologically Recent.

Typical stratigraphic relationships, applicable to the Porto Peter locality, are shown schematically in text-fig. 1. The oxbow deposits are in meandered channels incised into deposits that overlie a widespread erosion surface, frequently with a basal conglomerate. Fossil bones, usually dissociated and rolled, occur widely on that surface, and in all identifiable instances they include Pleistocene, and probably late Pleistocene, mammals. Oxbow deposits like that at Porto Peter thus can hardly be earlier than latest Pleistocene and most of them appear to be Recent, with ages more likely in hundreds than in thousands of years.

The Jesumira is far up the Môa drainage, toward the uplift of the Serra do Môa. The fossil locality is, however, the first exposure on the Igarapé Jesumira (i.e., is near the main river, the Môa) and is still in the "zona da baixada," where conditions are as along the Juruá and oxbows are still to be expected (Moura & Wanderley, 1938). The association of fossils is the same as at Porto Peter and the matrix is similar (Maury, 1937). Although we did not visit this area, it seems highly probable that that deposit is also a Recent oxbow filling.

Berry (1937) mentions unidentifiable plant fragments as from the "Tgaraje Agua Fuente," which is obviously a garbled version of Igarapé Agua Quente, another tributary of the Môa where Moura & Wanderley (1938) mention finding such remains. The nature and age of the deposit are not established. Berry also states that some of the identifiable plant material came from the Rio Amônea, a tributary that joins the Juruá at Taumaturgo. Berry gives no exact localities for any of the individual specimens described by him, but Maury, referring to the same specimens, explicitly ascribes all the named materials to Porto Peter. There are old oxbows along the Amônea and a deposit like that at Porto Peter could well occur, although we did not definitely identify one on the lower Amônea.



TEXT-FIG. 1.—Diagram of river bank exposure on the Upper Juruá, showing relationships of leaf-bearing clays to older deposits. A, laminated clays with abundant leaves and some mollusks, representing the filling of an oxbow lake exposed in river bank by a later meander. B, Pleistocene to Recent alluvial complex. C, Pre-Pleistocene beds (generally consolidated, nonlaminated clays and silts, without fossil leaves). Rolled fossils, often in a conglomerate of concretionary pebbles, are commonly found on or a short distance above the erosion surface between B and C. The fossils include middle to late Pleistocene mammals. The laminated clays, A, clearly cannot be older than late Pleistocene and in most cases, if not all, appear to be Recent.

Oliveira & Leonardos (1943, Fig. 156) show a locality on the Môa marked "Fauna pliocena (Formação Pebas)," which is clearly the Jesumira locality. They indicate "Flora pliocena" at Porto Peter and at Profeta (on the Juruá below Porto Peter). As they were following Maury, the Jesumira and Porto Peter localities should, on the authority followed by them, both have been referred to the Pebas formation, since the "fauna" (one or perhaps two incorrectly identified mollusks) is the same at both. The Profeta specimens are said by Oliveira & Leonardos also to have been collected by Moura & Wanderley, but I find no other reference to them.

The inescapable conclusion is that at present there is no valid evidence for the extension into Acre of the Pebas formation, or anything like it, and that the supposed Pliocene formation hitherto reported in that territory consists in fact of isolated patches

of deposits probably Recent and almost certainly not older than latest Pleistocene.

BROADER IMPLICATIONS

At Aquidaban, or Aquidabã, in the Territory of Amazonas on the middle Juruá, far below the area of our study, Moura & Wanderley (1938) made large collections of invertebrates and vertebrates. Roxo (1937) tentatively considered the invertebrates Pliocene but warned that they could be later, even Recent. The vertebrates are probably of mixed origin and may represent reworked concentrates of various different ages, as has certainly happened widely along the upper Juruá. They include Pleistocene, probably late Pleistocene, species and the beds containing them could be Pleistocene or Recent, certainly not Pliocene. This occurrence has been taken (e.g., by Oliveira & Leonardos, 1943) as indicative of extension of the same Pliocene formation as that of, for example, Porto Peter far down the Juruá below Acre and again as representing the Pebas formation. The former suggestion is incorrect, since no such formation is really known in Acre, and correlation with the Pebas of Peru is entirely gratuitous and highly improbable.

For almost a century there has been an accretion of evidence—or of legend—that a vast lake, estuary, or even arm of the sea occurred in Neogene times in the present upper Amazon basin. This idea has been built up by generalization from a number of isolated observations and by continual re-citation of more or less speculative older work. (For reviews and references to much of the very extensive literature see especially: de Greve, 1938; Rüegg & Rosenzweig, 1949; Paula Couto, 1956.) The present case of the "Pebas beds" of Acre, included in the supposed evidence by practically everyone who has considered this question since 1937, shows how such items may become unquestioned authority even though they never had any sound basis. The whole matter would seem to require reconsideration, but that is beyond the limits of the present note.

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THE GENERA *MICROAULOPORA* KUNTZ, 1895, AND *GUEMBELINA* KUNTZ, 1895, AND THE STATUS OF *GUEMBELINA* EGGER, 1899

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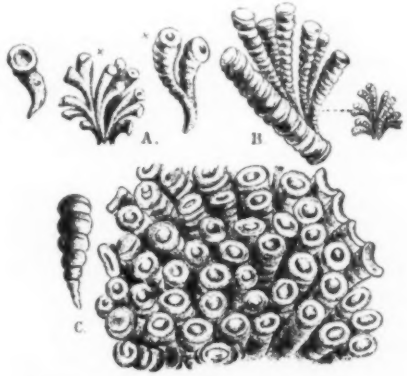
ABSTRACT—The Paleozoic chitinous micro-organisms *Microaulopora* Kuntz, 1895, and *Guembelina* Kuntz, 1895, are discussed on the basis of the original figures and descriptions. *Guembelina* Egger, 1899 (Foraminifera), recently shown to be a junior synonym of *Heterohelix* Ehrenberg, 1841, is thus doubly invalidated, in being also a junior homonym of *Guembelina* Kuntz, 1895.

GUEMBELINA KUNTZ AND MICROAULOPORA KUNTZ

IN 1895, Kuntz described two microscopic chitinous genera from Paleozoic coals. Although regarded originally as auloporoid corals, these are not mentioned in recent publications on corals (Piveteau, 1952, Moore, 1956) nor are they listed in Neave's Nomenclator Zoologicus, 1939, 1940, 1950. As they were neither included nor excluded, it is assumed that their publication has been overlooked by later workers. It is of further importance in that one of these genera, *Guembelina* Kuntz, 1895, is a prior homonym of the foraminiferal genus *Guembelina* Egger, 1899.

Kuntz (1895, p. 44–45) discussed the origin of coals, and in particular the work on this subject done by Gümbel (1883). Kuntz cited the occurrence of organic remains associated with the coals as evidence of their marine origin, attributing the absence of small calcareous groups to the carbonization process and its acidic byproducts. This process resulted in the destruction of all but the chitinous micro-organisms, but these were present in considerable abundance. Originally illustrated by Gümbel, these chitinous forms were reillustrated, described, and named by Kuntz (1895, p. 45–46, text-figs. A,B,C). These figures and descriptions are reproduced herewith (see text-fig. 1).

"Es sind offenbar zwei verschiedene Gattungen, die ich hier copire, wovon *Microaulopora* (Fig. A in 600 facher Vergrösserung) die Gestalt der vom Silur bis Carbon vorkommenden *Aulopora* hat, also dütenförmig cylindrische, zum Theil vereinigte chitinhaltige Individuen die aber 200–300 mal kleiner sind als bei *Aulopora*, während *Gümbelina* (Fig. B and C) aus ähnlichen aber bis dreimal grösseren und äusserlich ringsum gegliederten, scheibenartig geringelten Individuen sich corallenartig zusammensetzt. Tab. III, Fig. 53a, rechts, bei Gümbel (also excl. der Fig. 53 links, die vielleicht einer Jugendzustand ähnlich wie bei *Heteropora* darstellt) aus der Cännelkohle von Wigan in England (nach Gümbel darin häufig, aber auch in anderen Kohlen vorher von ihm gefunden) will ich *Microaulopora vulgaris* nennen. Hiermit ist offenbar identisch Fig. 55 aus der Bogheadkohle von Turbanhill, 'einen sehr beträchtlichen Theil der Kohle ausmachend' und Fig. 58 aus der permischen Plattelkohle von Böhmen, in der sie sich 'in geradezu erstaunlicher Häufigkeit' findet. Dagegen stellt Fig.



Chitinhaltige Halbcorallen aus Carbonkohlen.
A. Microaulopora vulgaris. (⁶/₁°.)
B. Gümbelina ruthenica. (⁶/₁° + ¹²/₁°.)
C. Gümbelina tasmanica. (⁶/₁°).

TEXT-FIG. 1—Copy of text figures from Kuntz, 1895 (reduced to 0.9 times the size in the original publication).

64, rechts, bei Gümbel (die Figur links als undeutlich ist auszuschliessen), welche ich hier unter B in nur 400 facher Vergrösserung für die grosse Figur, die kleine entsprechend kleiner reproducire, *Gümbelina ruthenica* aus den devonischen braunen russischen Steinkohlen von Tschulkowa bei Tula vor, wo sie in 'enormen Massen' vorkommt, sie hat 'uhrglasähnlichen' Aufbau. Fig. 57 bei Gümbel, hier Fig. C, bei 400 facher Vergrösserung, ist *Gümbelina tasmanica* mit zweierlei, zum Theil dünnen schmalen, zum Theil doppelt dickeren, wulstigen, äusserlichen Abgliederungen, aus der Tasmanit-Gaskohle von Van-Diemensland, 'worin sie in höchst beträchtlicher Menge vorhanden sind.' Wir haben es hier wahrscheinlich mit einer ausgestorbenen besonderen Familie, chitinhaltigen Halbcorallen, zu thun, die zwischen Foraminiferen und Corallen steht" (italics ours).

Thus, *Microaulopora* is described as being horn-shaped, sometimes multiple, with chitinous structure, resembling the Paleozoic coral genus *Aulopora* but 200 to 300 times as small. The type of the genus (fixed by monotypy) is *Microaulopora vulgaris* which occurs in the cannel coal of Wigan, England.

The genus *Guembelina* is of similar appearance, but annulated, with the separate individuals about three times as large, and occurring generally in colonies. Two species were described, *G. ruthenica*, which occurs in "enormous masses" in the Devonian coals of Tschulkowa in Russia, and *G. tasmanica*, a dimorphic form with part of the individuals thin and small, and the remainder larger and thicker. The latter species was found in abundance in the Tasmanite gas coal of Van Diemensland. *Guembelina tasmanica* Kuntz, 1895 (p. 46) is here designated as type species of the genus *Guembelina* Kuntz, 1895.

As to the affinities of these genera, Kuntz stated that they probably represented a distinct and extinct family of "semicorals," which he regarded as intermediate between Foraminifera and corals.

In view of the considerable current interest in palynology, it is quite possible that these chitinous genera will be found elsewhere in similar occurrences. Probably unrelated to either Foraminifera or corals, these genera may possibly have affinities with the chitinozoans, which are proving to have stratigraphic importance in early Paleozoic strata. Described by Kuntz as occurring from the Devonian to the Permian, they might be later colonial developments from the earlier solitary chitinozoans, although little is yet known of the internal structure of these forms. The individuals are much smaller, and apparently they did not have the characteristic apertural collar of the true chitinozoans.

Priority of Guembelina Kuntz, 1895, over Guembelina Egger, 1899

The prior status of *Guembelina* Kuntz, 1895, invalidates the use of the name *Guembelina* Egger for the foraminiferal genus of the family Heterohelicidae. Independent studies by Hofker (1957) and Montanaro Gallitelli (1957) both concluded that species previously referred to the genera *Heterohelix* Ehrenberg, 1841, and *Guembelina* Egger, 1889, have no morphologic distinction. The separation of the forms with large early planispiral coil as *Heterohelix* (the type genus of the family), and those with very small coil (in the microspheric generation), or no coil, as *Guembelina*, was regarded as untenable by both Hofker and Montanaro Gallitelli, although their interpretations and conclusions differed somewhat.

Montanaro Gallitelli (1957, p. 137–138) studied numerous individuals of many species, and found that from 0.5 to 80.0 per cent of the specimens of the various species of "*Guembelina*" had an early coil, averaging 8.2 per cent coiled in over 3000 specimens examined. Nearly all species, except those from the Lower Cretaceous, showed an early coiled stage.

Hofker (1957, p. 421) studied *Guembelina striata* and *Heterohelix navarroensis* (which he regarded as synonymous) from the Turonian to Maestrichtian of northern Germany and Holland and concluded that the size of the proloculus of the specimens decreased in the younger geologic ages. According to Hofker, the coiled versus biserial development was not due to dimorphism, with the coiled specimens representing a microspheric generation, for in the later Upper Cretaceous, Hofker stated that *Guembelina* became apogamous, the smaller proloculi indicating the presence of a single

generation—the microspheric one. He concluded (1957, p. 423) "Es ist also wahrscheinlich besser, den Namen *Heterohelix* gänzlich fallen zu lassen." This suggestion cannot be followed, as the laws of priority require the retention of the oldest valid name—in this case, *Heterohelix*.

This decision, contrary to that of Hofker, was reached by Montanaro Gallitelli, who regarding *Heterohelix* and *Guembelina* as synonymous, stated (1957, p. 138) that, "As *Heterohelix* has priority, the name *Guembelina* must be considered a junior synonym."

The name *Guembelina* Egger, 1899, is thus doubly invalidated for use in the Foraminifera, first as a junior homonym of *Guembelina* Kuntz, 1895, and secondly as a junior synonym of *Heterohelix* Ehrenberg, 1841. *Heterohelix* was amended by Montanaro Gallitelli to include species previously assigned to *Guembelina*, and the names of the family Heterohelicidae, and subfamily Heterohelicinae, based on *Heterohelix* as type genus, remain unchanged.

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JOURNAL OF PALEONTOLOGY, V. 35, NO. 3, P. 628–635, 8 TEXT-FIGS, MAY, 1961

PALEONTOLOGICAL NOTES

TYPE SPECIMENS OF NORTH AMERICAN PALEOZOIC RADIOLARIA

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In connection with our current studies of Paleozoic radiolarian assemblages from the Devonian of Ohio (Foreman, 1959) and Western Australia (Glenister & Crespin, 1959) and the Silurian of the Canadian Arctic Archipelago, we have had occasion to examine type material of two assemblages of Paleozoic Radiolaria previously described in the United States (Ruedemann & Wilson, 1936; Aberdeen, 1940). Apart from direct comparisons of the species in these previously described assemblages with forms in our undescribed material, which will be discussed in subsequent papers, we have made certain incidental observations which it seems appropriate to report in this separate note. Our examination of Ruedemann and Wilson's material in the New York State Museum at Albany, N. Y. was made possible by the cooperation of Dr. Donald W. Fisher and his staff, and Aberdeen's material in the Walker Museum of Paleontology at the University of Chicago was kindly loaned to us by Dr. J. Marvin Weller and Matthew H. Nitecki. For one of us (H.P.F.), this represents part of a research project supported by a grant from the Geological Society of America.

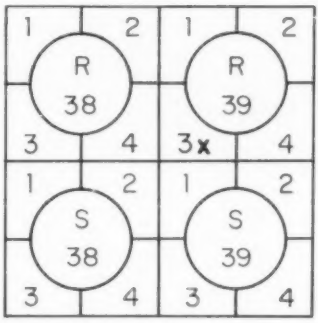
At least some of the structures in the Ordovician Normanskill and Deepkill cherts of New York on which Ruedemann and Wilson based their radiolarian descriptions may well represent Radiolaria, but they are not sufficiently well defined to warrant the reconstructions and identifications which those authors made.

Aberdeen's Radiolaria from the Santiago chert member of the Caballos novaculite of Texas, on the other hand, are well preserved and must be taken into account for comparative studies. One of our principal objects in examining this type material was to determine whether certain structures which have recently been found commonly in a few widely separated Silurian to Carboniferous localities might have been overlooked during the original description—namely, members of the genera *Palaeoscenidium* Deflandre and *Ceratoikiscum* Deflandre, and the presence within many of the Sphaerellaria of spicular structures similar to those described by Hinde (1899) as occurring within several species from the Devonian of New South Wales including his *Staurosphaera pusilla* and *Acanthosphaera etheridgei*. We have confirmed that none of these occur in Aberdeen's material.

In searching for Aberdeen's type specimens, we have become aware of some discrepancies between the positions of the type specimens as given in her text, and those indicated in the legends to the plates. We therefore record, under the specific names below, the positions of type specimens as we have found them on the slides. The relative abundances of the species are also noted, together with observations which amplify the original descriptions.

The positions of type specimens were marked by Aberdeen in India ink on the cover glasses or lower surfaces of the slides. Although these markings have been preserved fairly well through the past twenty years, it seems desirable to supplement them by coordinates, the future reliability of which is not so dependent upon careful handling of the slides. For this purpose we have used an England Finder, made by Graticules Ltd., 57/60 Holborn Viaduct, London E.C.1, and distributed in the U. S. by Eric Sobotka Co., 110 West 40th Street, New York 18, N.Y. and Edmund Scientific Co., 101 Gloucester Pike, Barrington, New Jersey. This Finder is a 3″×1″ glass slide on which is centered a grid 73 mm.×24.5 mm. divided into approximately 1 mm. squares (75×25). The squares are marked in such a way that when viewed through a compound microscope the vertical rows are numbered 1 to 75 from left to right, and the horizontal rows are lettered A to Z (excluding 1) from top to bottom. Each square is subdivided

into five parts, four of which are labelled 1 to 4 and the fifth may be designated 0 (text-fig. 1). When it is wished to record the position of a specimen, the slide bearing the preparation is placed in the holder of a mechanical stage and the desired specimen centered in the field of view. The slide is then removed and replaced by the Finder. The position is recorded according to the numbered and lettered subdivisions of the grid: thus the location of a specimen in a position corresponding to X in text-fig. 1 would be recorded as R39/3. Two adjacent edges of the Finder and the corresponding edges of the slides bearing the specimens are reference edges, and these vary with different mechanical stages: for the purposes of the present work, the reference edges are the short edge of the slide on the observer's right hand, and the long edge nearer the observer. Both Finder and specimen slide are placed on the microscope stage so that their labels (viewed normally, not through the microscope) are in the normal reading position. In the following notes, the positions of specimens follow the slide numbers in parentheses.



TEXT-FIG. 1—Portion of the grid of an England Finder. X marks position R39/3.

TYPE SPECIMENS OF ABERDEEN'S RADIOLARIA

References to figures on plates are to those of Aberdeen (1940).

"Thallassicollidae."—Figured specimen (Pl. 20, fig. 1), slide 44537 (K26/0). Other figured specimens (Pl. 20, figs. 2 and 3) not found.

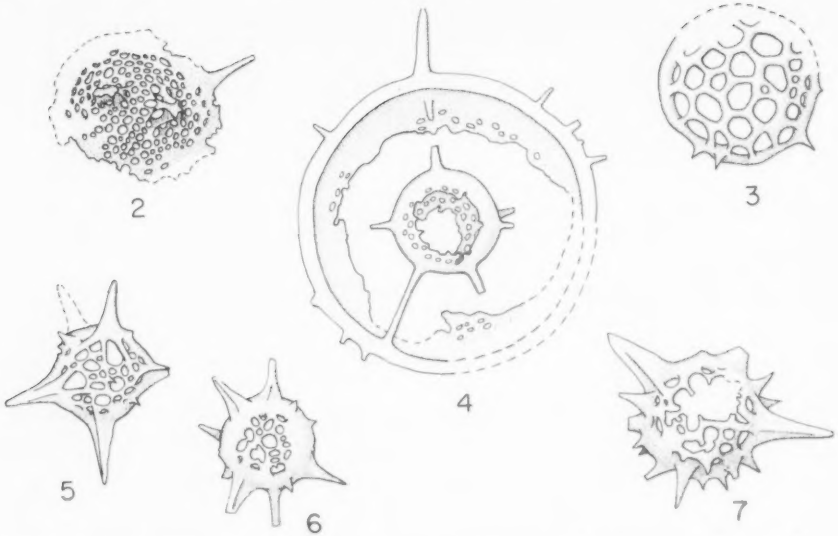
Cenosphaera variabilis.—Syntype (Pl. 20, fig. 17), slide 44496 (M30/3). Unfigured syntype on slide 44997 not found. The figured syntype has at least three spines, two of them broken off and one 60 μ long, arising from tent-like protuberances on the shell surface (text-fig. 2): the bases of the two broken spines are visible in Aberdeen's published figure. The species is apparently rare—the only specimen which we have been able to identify positively is the figured syntype.

Cenosphaera hexagonalis.—Holotype (Pl. 20, fig. 12), slide 44999 (T34/0). Paratype (Pl. 20, fig. 13) on slide 44995 not found. This species is not uncommon. Many specimens have short, acute spines arising from the lattice surface (text-fig. 3; slide 44494, H33/4). The specific name is preoccupied by *Cenosphaera hexagonalis* Haeckel, 1887.

Cenosphaera semiequalis.—Syntype (Pl. 20, fig. 7), slide 44538 (N22/4). Syntype (Pl. 20, fig. 8), slide 44998 (D33/2). The syntype on slide 44538 shows distinctly the bases of three rod-like spines originating from the lattice surface: the other syntype is not sufficiently well preserved to show presence or absence of external spines. Skeletal fragments which may belong to this species are rather common.

Carposphaera magna.—Syntype (Pl. 21, fig. 4), slide 44545 (R27/0). Syntype (Pl. 21, fig. 10), slide 44535 (T27/0). The remaining syntype (Pl. 20, fig. 18) is probably the specimen on slide 44493, at coordinates 043/2 when the slide is turned over so that the cover glass is downward. The ratio of the diameters of inner and outer lattice shells, on the basis of which this species is distinguished from *Carposphaera equalis*, grades to those proportions described as characteristic of the latter species. The specific name is preoccupied by *Carposphaera magna* Rüst, 1892.

Carposphaera equalis.—Syntype (Pl. 20, fig. 4), slide 44532 (F28/3). Syntype (Pl. 20, fig. 5), probably slide 44535 (E30/2). As indicated in the preceding paragraph, it is impossible to distinguish this species reliably from *Carposphaera magna*. Taken together, the two forms are common in the assemblage. Many specimens which apparently belong to this species have rod-like external



TEXT-FIGS. 2–7—Radiolaria from Aberdeen's preparations of the Caballos novaculite. All figures ×150. 2, *Cenosphaera variabilis;* 3, *Cenosphaera hexagonalis;* 4, *Carposphaera equalis;* 5, *Hexastylus basiporosus;* 6, *Hexastylidium variatum;* 7, *Heliosphaera macrospinosa.*

spines (text-fig. 4; slide 44491, R22/0).

Thecosphaera hexpenetrata.—Holotype (Pl. 21, fig. 16), slide 44536 (M27/0). The holotype is the only specimen found.

Rhodosphaera sp.—Figured specimen (Pl. 20, fig. 10), slide 44547 (T28/3). It is doubtful that this species can be reliably distinguished from those described in the genus *Spongoplegma.*

Plegmosphaera spiculata.—Holotype (Pl. 21, fig. 3), slide 44532 (Q29/0). Unfigured paratype, probably slide 44497 (B38/0). Apart from the absence of a medullary shell and associated radial beams, this form resembles those described in the genus *Spongoplegma.* Specimens lacking these inner structures are common, but it is doubtful whether this is significant or whether it is due to vagaries of the type of preservation of the radiolarians in this material—coating or replacement of the original silica by iron oxide.

Spongoplegma brevisphaera.—Syntype (Pl. 21, fig. 17), slide 44542 (N32/4). Unfigured syntype, probably slide 44538 (L33/4). The specimen believed to be the unfigured syntype has distinct radial beams between the inner and outer surfaces of the spongy cortical region: these are shorter than those described for *Spongoplegma longispinosa,* but otherwise similar.

Spongoplegma longispinosa.—Syntype (Pl. 20, fig. 6), slide 44546 (H42/2). Syntype (Pl. 21, fig. 1), slide 44998 (R32/0). The width of the spongy region, and the length of the radial beams within it, are variable between those described for this species and for *Spongoplegma brevisphaera.* Taking these two species together, they are common in the assemblage.

Xiphostylus inclinatus.—Syntype (Pl. 21, fig. 7), slide 44548 (E43/1). Syntype (Pl. 21, fig. 8), slide 44494 (H36/0). This species is apparently not uncommon, though it is of course impossible to recognize except in those sections which are longitudinal.

Stylosphaera quasiobtusa.—Syntype (Pl. 21, fig. 5), slide 44544 (S34/4). Unfigured syntype, probably slide 44998 (M26/0). Besides the syntypes, three specimens were found.

Staurostylus varispinatus.—Holotype (Pl.

20, fig. 19), slide 44997 (P40/3). The holotype is the only specimen found. The classification of this specimen is regarded as quite doubtful, because the object which Aberdeen regarded as the short spine might equally well be a fortuitously apposed dark grain of inorganic origin.

Staurosphaera rotunda.—Holotype (Pl. 20, fig. 11), slide 44548 (P36/3). As the specimen is incomplete, its determination as a staurosphaerid rather than a cubosphaerid seems somewhat doubtful. The holotype is the only specimen found.

Staurodoras brevispinosa.—Holotype (Pl. 21, fig. 11), slide 44546 (M34/3). The lattice shell is thick-walled, but we see no evidence that it is spongy as described. Most of the pores of the lattice-shell are approximately 5 μ in diameter. The holotype is the only specimen found.

Hexastylus basiporosus.—Syntype (Pl. 21, fig. 6), slide 44546 (J42/3). Syntype (Pl. 21, fig. 9), slide 44542 (N37/2). Syntype (Pl. 21, fig. 13), slide 44495 (R24/3). Unfigured syntype, possibly slide 44549 (Q36/4). Unfigured syntype, probably slide 44537 (Q37/4). This species is common. Many specimens have by-spines arising from the lattice shell (text-fig. 5; syntype figured by Aberdeen on Pl. 21, fig. 13) and thus approach *Heliosphaera macrospinosa*. The number of main-spines is not constantly six, but may also be five or seven. Diameter of lattice shell generally 90–120 μ.

Hexastylidium variatum.—Holotype (Pl. 21, fig. 14), slide 44545 (S39/3). It is impossible to reconcile the description of this species with the specimen figured as its holotype. Examination of both sides of the holotype reveals that six or perhaps seven, almost complete spines (each approximately 35 μ long) are present, together with the bases of at least two others (text-fig. 6: the structure which may be a seventh complete spine is not visible in this figure, as it is on the side of the specimen away from the observer).

Hexalonche sp.—Figured specimen (Pl. 20, fig. 9), slide 44997 (N37/2). The figured specimen is the only one found. It is not sufficiently well preserved to permit its certain identification as *Hexalonche*.

Acanthosphaera dodecaspinosa.—Syntype (Pl. 21, fig. 2), slide 44538 (028/0). Syntype (Pl. 21, fig. 15), slide 44535 (P29/1). Syntype (Pl. 21, fig. 18), slide 44548 (L25/0). In many specimens, the lengths of the spines approximate or exceed the diameter of the lattice shell. This species is apparently common: most of the specimens are fragmentary.

Acanthosphaera microspinosa.—Holotype (Pl. 20, fig. 21), slide 44535 (M34/4). Spines on the holotype range up to 40 μ in length. The species is rather common.

Acanthosphaera hirsuta.—Holotype (Pl. 21, fig. 12), slide 44543 (T36/4). This species is rather common.

Acanthosphaera grandispinosa.—Holotype (Pl. 21, fig. 19), slide 44547 (J28/1). The holotype is the only specimen positively identified.

Heliosphaera macrospinosa.—Holotype (Pl. 20, fig. 14), slide 44498 (F36/2). Examination of the holotype, particularly the side opposite that from which Aberdeen's photograph was taken (text-fig. 7), shows that this species closely resembles *Hexastylus basiporosus* with strongly developed by-spines. This species, if it be distinguished from *H. basiporosus* by its strongly developed by-spines, is rather common. Diameter of the lattice shell generally 95–120 μ.

Heliosphaera alternata.—Holotype (Pl. 20, fig. 22), slide 44545 (N28/0). Two of the main-spines of the holotype are about 220 μ long. Several specimens of this species were found.

Haliomma perfecta.—Syntype (Pl. 20, fig. 20), slide 44546 (Q35/0). Syntype (Pl. 20, fig. 16) not found. Unfigured syntype on slide 44537 not found. Few specimens of this species were found.

Astrophacus cingulatus.—Holotype (Pl. 20, fig. 15), slide 44996 (C34/2). The holotype is the only specimen found. There is no strong evidence for the outer shell being lenticular rather than spherical: if it is spherical, this species may be the same as *Carposphaera equalis*.

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Contribution from Scripps Institution of Oceanography.

MANUSCRIPT RECEIVED JUNE 9, 1960

THE LOWER DENTITION OF *PROTERIX LOOMISI* MATTHEW?

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A lower jaw (South Dakota School of Mines Museum of Geology Number 55140) from near the top of the Brule formation in Shannon County, South Dakota, may be referable to *Proterix loomisi* Matthew. The specimen was found at the Godsell Ranch locality (S.D.S.M. No. V5411) ten feet below the contact of the Brule and younger channel deposits. At this point the upper forty feet of the Brule has been removed by very early Miocene stream action which has left a thick series of early Miocene channel deposits lying disconformably on the Brule. These stream deposits may be considered as part of the Sharps formation, representing a facies similar to the Gering formation of Nebraska.

It is suggested that this jaw may represent *Proterix loomisi* Matthew. It is referable to the Echinosoricinae, as evidenced by the similarity of its dentition to that of *Echinosorex* De Blainville from the Recent of southern Asia. The Godsell Ranch locality is close, both temporally and geographically, to the type locality of *P. loomisi*. The type of this species is a partial cranium (A.M.N.H. No. 9756) which was found in the upper part of the Brule formation in Indian Draw; this is in the White River Badlands, a few miles away from the S.D.S.M. locality.

The fragment contains the P_3-M_1. The P_3 is small and conical; the anterior face is convex and the posterior face concave; there is an intermittent cingulum. The P_4 has a large conical anterior cusp with the posterior face flattened; extending halfway up the face from the antero-lingual corner of the tooth is a small ridge which has developed from a spur of the cingulum; the posterior flattening of this cusp is in part due to wear; behind the principal cusp is the worn remnant of a trenchant "heel" which had its crest slightly linguad of the center line when unworn; there is a well developed cingulum extending from the anterior midline around the labial side, across the posterior end of the tooth and anteriorly along the lingual side to the posterior base of the

TEXT-FIG. 1—*?Proterix loomisi* Matthew, S.D.S.M. No. 55140. Fragment of right ramus with P_3-M_1 and a fragment of M_2. Labial and crown views. ×5.

principal cusp. The M_1 has a strongly developed trigonid and talonid; the trigonid is heavily worn, the paraconid is small and compressed anteroposteriorly, the protoconid is large and triangular, the metaconid is large and round with a flattened posterior side, the valley between the paraconid and the metaconid is narrowed lingually by the expansion of the metaconid and expands into a shallow "Y" at its labial end; the talonid has a large triangular shaped hypoconid which is broadly connected posteriorly with a large antero-posteriorly compressed entoconid; anteriorly the hypoconid is connected by its angular anterior edge to the middle of the posterior face of the protoconid; the talonid valley is slightly constricted lingually but large; the cingulum is strongly developed from the antero-lingual corner of the paraconid along the labial side to the base of the hypoconid; the cingulum is also well developed across the posterior end of the tooth with an expansion at the base of the hypoconid that may represent an incipient entoconulid. Part of the trigonid of the M_2 is preserved; it resembles that of the M_1 except for a greater reduction of the paraconid and a greater labial expansion of the valley between the paraconid and the metaconid.

TABLE OF MEASUREMENTS
(In Millimeters)

P_3	anteroposterior diameter	1.90
	transverse diameter	1.79
P_4	anteroposterior diameter	3.30
	transverse diameter	2.70
M_1	anteroposterior diameter	4.50
	transverse diameter	3.60
M_2	transverse diameter (trigonid)	3.20
P_3—M_1		9.10

The drawings were made by Dr. Florence D. Wood.

ADDITIONAL NOTE ON OVOVIVIPAROUS *TURRITELLA*

KATHERINE V. W. PALMER

After publishing the note on "Viviparous *Turritella pilsbryi* Gardner" (Palmer, Jour. Pal., v. 32, No. 1, p. 210–213, 1958), attention was called by Robert V. Kesling to an article in 1935 on "Ovoviviparous reproduction of Miocene Turritellidae," by A. H. Sutton (Amer. Mid. Nat., v. 16, No. 1, p. 107–109) Dr. Sutton found and reported a shell of *T. alumensis* Mansfield from Alum Bluff, Florida, Choctawhatchee formation, Miocene. This specimen contained 48 young. The discovery furnishes information on a fourth species of *Turritella* from the Chesapeake and Floridian Miocene which probably had an ovoviviparous habit of reproduction.

RECENTLY DESCRIBED BIRDS AND MAMMALS FROM CUBAN CAVES

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Pleistocene fossils collected by members of the Sociedad Espeleológica de Cuba have served as the basis of several new generic and specific names of birds and mammals and have given rise to a rumor of the former occurrence on that island of giant flightless birds allied to *Phororhacos* of the Tertiary of Argentina (Arredondo, 1954, 1955, 1956, 1958a, 1958b; Koopman, 1958). As the descriptions are in journals likely to be

overlooked by specialists, and particularly since the type series of the supposed phororhacid consists of a mixture of bird and mammal bones, their status in nomenclature is reviewed at this time.

THE JOURNALS

The three Cuban periodicals known to contain reference to this material are the Sociedad Espeleológica de Cuba Boletiń, Bohemia, and El Cartero Cubano. For their kind cooperation in supplying copies I am much indebted to Sr. Oscar Arrendondo and to the editorial staffs of Bohemia and El Cartero Cubano.

The S.E.C. Boletiń is a brochure of loosely stapled typewritten sheets that are reproduced by the "Ditto" stencil process with purple ink that fades quite away upon exposure to light. It is said to appear monthly from offices at Egido and Misión streets, La Habana. It is apparently not on sale, but a statement soliciting exchanges appears on the cover. Because of the ephemeral method of reproduction, if for no other reason, these sheets do not satisfy the requirements for the publication of new scientific names.

Bohemia is an illustrated weekly review, founded in 1908. It is published at Trocadero 357–359, La Habana, where it is on sale at 15 centavos per current number, 25 centavos for back numbers. Fossils have been described and illustrated in this magazine, but no new names appear to have been proposed in it.

El Cartero Cubano is the official organ of the Asociación Nacional de Carteros. It is published monthly at Revillagigedo 115, La Habana, where it is on sale at 20 centavos per number and is distributed by exchange to allied organizations throughout the continent and in Spain. It is printed by standard methods on good quality paper. If otherwise valid, new names proposed in this journal have standing in nomenclature, particularly since the author distributed excerpts of his papers to at least five workers abroad.

THE SUPPOSED PHORORHACIDS

For alleged phororhacid material from Cuba, Arredondo (1958a, p. 11) has proposed the generic name *Ornimegalonyx* and the specific names *Ornimegalonyx Arredondoi* and *Ornimegalonyx Oteroi*. These names are proposed in a valid manner, since they are published in a printed journal available to the public, with a diagnosis, and with the material illustrated by photograph and drawing. I hereby designate *Ornimegalonyx oteroi* as type of the genus.

The name *Ornimegalonyx arredondoi* is said (Arredondo, 1955, 1956, 1958a) to have been proposed provisionally on June 8, 1954, but this is merely a quotation from a letter sent by Arredondo on February 11, 1954, to Dr. M. Rivero de la Calle and mentioned in the minutes of the S.E.C. under date of June 8, 1954. It does not constitute publication. The first appearance in print of the name *Ornimegalonyx arredondoi* seems to be in the article in El Cartero Cubano cited above (Arredondo, 1958a). Here Arredondo states that he now declines the name *arredondoi* and substitutes in its place that of *oteroi*.

The material on which the two specific names are based is the same. It consists of a fragmentary femur, three fragments of a tibiotarsus, a fragmentary tarsometatarsus, two ungual phalanges, and two subterminal phalanges, collected by Arredondo on January 2, 1954, in the Cueva Pío Domingo, Valle de Pica Pica, Sierra de Sumidero, province of Pinar del Río, Cuba. The type series is illustrated in the upper right-hand photograph on page 12 of the Cartero Cubano article cited above. A somewhat better reproduction of the same photograph, turned around, appears in the upper right-hand illustration on page 48 of the Bohemia article (Arredondo, 1954).

The type series represents a large owl of the family Strigidae. The family reference is shown by the presence of an ossified bridge over the proximal end of the extensor groove of the tarsometatarsus. Because of the possibility that more than one individual or taxon may be represented in the type series, the left tarsometatarsus is hereby selected as lectotype of both *Ornimegalonyx oteroi* and *Ornimegalonyx arredondoi*. These two names are of equal date, as demonstrated above. Under the first reviser principle I select *Ornimegalonyx oteroi* as the name of the species. Alleged members of the Phororhacidae, said to represent about four species, have been reported (Arredondo, 1955, p. 4, 26, 28; Arredondo, 1956, p. 5 of appendix;

Arredondo, 1958a, p. 10, 12; Koopman, 1958, p. 2) from other Cuban localities indicated on a map in the S.E.C. Boletín (Arredondo, 1955, p. 4). From the evidence available none of this material belongs in the Phororhacidae but appears likewise to be strigiform.

RECENTLY DESCRIBED RODENTS

Attention is also called to the publication of several new names of Pleistocene rodents (Arredondo, 1958b). These are as follows:

1. *Geoboromys*, p. 11 and fig. 2 of lower cut on same page. Described in family "Echimydae." The name is a nomen nudum at this point, for although the lower cheek teeth are figured and described, no species is named. The locality of the figured specimen is Cueva P/o Domingo; numerous other localities are mentioned. The name *Geoboromys* was used in connection with a new specific name, the second declension, genitive singular of the patronym Rivero, in the S.E.C. Boletín (Arredondo, 1956, p. 7 of appendix, figured on p. 22 and on p. [10] of appendix), but as already shown, that brochure fails to satisfy the requirements of publication.

2. *Macrocapromys*, p. 10, 48. Described in family "Capromydae." Type by monotypy, *Macrocapromys acevedo* Arredondo.

3. *Macrocapromys Acevedo*, p. 48, fig. 1 of upper left-hand cut on p. 10. Type locality, Cueva San José de las Lamas, in Santa Fé, province of Habana. Described on a humerus. In the two copies seen, the specific name is illegally corrected in longhand to *Acevedoi*.

4. *Geocapromys columbianus pleistocênica* [sic], p. 48, fig. 1 of lower right-hand cut on p. 10. Type locality not stated. Described on lower jaw characters. The name was previously proposed, without accent but likewise with incorrect gender, in the S.E.C. Boletín (Arredondo, 1956, p. 37, fig. on p. 38), a medium not satisfying the requirements for publication.

5. *Capromys intermedius*, p. 48, fig. 2 of upper cut on p. 11. Type locality not stated. Provisionally described on mandibular characters.

With the exception of *Geoboromys* all of the above names are validly proposed.

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JOURNAL OF PALEONTOLOGY, V. 35, NO. 3, P. 636, MAY, 1961

CORRECTION

NOTE ON SOME SPECIES OF OSTRACODA DESCRIBED BY A. M. NORMAN, A CORRECTION

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Louisiana State University

In a "Note on some species of Ostracoda described by A. M. Norman," Jour. Paleontology 34, no. 3, May 1960, I indicated the date of A. M. Norman's "Report on the Crustacea" in G. S. Brady, "Reports of Deep Sea Dredging on the Coasts of Northumberland and Durham, 1862–1864," Natural History Transactions of Northumberland and Durham, being papers read at the Meetings of the Natural History Society of Northumberland, Durham and Newcastle-on-Tyne and the Tyneside Naturalists' Fieldclub, 1865–1867, v. 1, as 1867, because that is the date appearing on the title page. However, as H. V. Howe in his "Handbook of Ostracod Taxonomy," Louisiana State University Studies, Physical Science Series Number One (1955) remarks, it appears that the parts for the different years were originally published separately. Sars in "Oversigt af Norges marine Ostrakoder," Vorhandlinger i Videnskabs-Selskabet i Christiania 1865," which bears the publishing date 1866, gives on page 130 a list of Norman's species that came to his notice after the manuscript was handed in for printing. This list makes it clear that Norman's paper was published before Sars' and unless this last paper was not published until some much later date, we cannot accept an 1867 date for Norman's publication.

This does not alter the sequence in which Brady's and Norman's contributions, discussed in the "Note," were published, but the date on Norman's paper should be changed from 1867 to 1865.

JOURNAL OF PALEONTOLOGY, V. 35, NO. 3, P. 637, MAY, 1961

NOTICES

INQUA MEETING TO BE HELD IN POLAND AUGUST—SEPTEMBER, 1961

The International Association for Quaternary Research (INQUA) will meet in Poland during the late summer of 1961. The Congress, which meets every four years, will be preceded by an excursion starting from Warsaw on August 27. The first meeting of the Congress will take place on September 2 and the last meeting on September 7. A post-Congress excursion will be held from September 7 to 21 and will visit the main localities containing Polish Quaternary deposits.

INQUA was first organized during an international geological meeting in Copenhagen in 1928 for the purpose of approaching Quaternary problems on an interdisciplinary level particularly in the fields of geology, archaeology, climatology, and chronology. Although the Congress has been attended primarily by Europeans, it is international and non-Europeans are urged to attend.

It has been the desire of many Europeans and Americans to hold the Congress in the United States sometime in the future. To this end the National Academy of Sciences-National Research Council created a U. S. Committee on INQUA. This Committee is making plans to invite the next Congress to meet in this country during the late summer of 1965.

All persons interested in the 1961 Congress in Poland may obtain more detailed information by writing to the following:

Professor Rajmund Galon
Secretary General, INQUA
Geographical Institute
University
Tourń, Poland

CINCINNATI MEETINGS

The paleontology program at the Cincinnati meetings of the Society next November promises to be unusually interesting, even when seen thus far in advance. The Society will endeavor to celebrate the role of old Cincinnati in the history of American paleontology, with several special features designed with this in mind. The Committee would like to see an unusually strong program of paleontologic papers *in all aspects of paleontology* offered at these meetings, and invites all paleontologists to participate through papers and attendance. Palecology and Paleontology of the Cincinnati Arch area will be special features of the program. Abstracts may be secured from the Secretary of the Geological Society of America (417 W. 117th St., New York 27, N.Y.), the Secretary of the Paleontological Society or the undersigned. The dead-line for abstracts is early July.

KENNETH E. CASTER, CHAIRMAN,
P.S. Program Committee

JOURNAL OF PALEONTOLOGY, V. 35, NO. 3, P. 638–639, MAY, 1961

REVIEW

REVIEW OF "THE PALEOCENE PANTODONTA" BY ELWYN L. SIMONS, TRANSACTIONS, AMERICAN PHILOSOPHICAL SOCIETY, NEW SER., V. 50, PT. 6, 99 P., 18 FIGS., JULY, 1960, PRICE $2.50.

Complete skeletons of early Cenozoic mammals are exceedingly rare. Therefore the relatively large Paleocene Pantodonta, now remarkably well represented by a number of nearly complete skeletons of many species, are of special interest revealing the postcranial osteology of a primitive but already diversified group of early placental mammals at a time when the latter had just begun their wide Cenozoic adaptive radiation.

Simons briefly reviews earlier work on pantodonts, then treats the taxonomy, general skeletal anatomy, stratigraphic occurrence, ecology and phylogenetic relationships of the order.

The Pantodonta and Dinocerata (uintatheres) once were united in the Amblypoda, but Simons, reaffirming the distinctness of the two groups, attributes their similarities to convergence thus following Simpson and others. A new superfamily, Pantolambdoidea, is erected and diagnosed for reception of the relatively primitive Pantolambdidae, the Barylambdidae and the Titanoideidae. The Coryphodontidae, a late lingering family, is placed in the new, monotypic superfamily Coryphodontoidea. The systematic portion of the paper includes lists of types and stratigraphic distributions as well as diagnoses and discussions for the North American families, genera and most species; a useful, judicious compilation and evaluation of a great deal of widely scattered information to which are added many new observations. Obviously not intended as an encyclopedic treatment, this section can be supplemented from the very adequate list of references.

Two exclusively Old World genera, *Eudinoceras* and *Hypercoryphodon*, are briefly considered. Although both are younger than Paleocene, a more detailed treatment of these would have made the revision more nearly complete.

"*Procoryphodon*" Flerow from the Gashato formation of Mongolia is reduced to synonymy with *Phenacolophus* (a condylarth, *incertae sedis*) from the same formation.

The Asiatic Pantolambdodontidae are removed from the Pantodonta to the protungulates *incertae sedis*.

Archaeolambda planicanina Flerow, 1952, an Asiatic species, is summarily thrown into synonymy with *Haplolambda* Patterson, 1939, eliminating the monotypic Archaeolambdidae. Although this action may have been justified it should have been supported by at least some discussion.

Although the 18 figures (65 subfigures) mainly illustrate dentitions, these are the skeletal parts most commonly encountered and stratigraphically most useful. Descriptions of other skeletal parts can be supplemeted by reference to illustrations in earlier publications.

Coryphodon, mainly an Eocene form, receives only partial treatment but revision of that genus is a work in itself presently being undertaken by the same author. Members of this genus are very large animals, described "species" excessively numerous, and the many specimens widely scattered throughout collections. Revision of this group is much needed for its stratigraphic value but would have needlessly delayed this broader work. Unfortunately the author, succumbing to a temptation he explicitly recognized, described still another, supposedly *most* primitive species *C. proteus* based on material from the Clarkforkian (latest Paleocene) of Montana.

The detailed resume of the pantodont skeleton offers an interesting picture of the osteology of these primitive placentals.

The first conclusion reached in the paleoecology section is that the nature of the sedimentary deposits in which pantodonts have been found reveals little concerning the habitat preferences of the animals. Morphological peculiarities of the limbs, feet, tail and to some extent the teeth are more helpful, suggesting an early adaptive radiation of this primitive placental group. Simons reaches several tentative conclusions here. *Titanoides*, with its claws, heavy forelimb

and shoulder development is viewed as a root-digging vegetarian much like the later chalicotheres. He suggests that at least some barylambdids, with their compressed tails, mobile forearms, and small hooves on splayed digits may have been semiaquatic swimmers and marsh dwellers. *Pantolambda* and *Ignatiolambda*, with small hooves on splayed digits are considered riparian forms; *Coryphodon* a river dwelling, root pulling creature of hippo-like habits.

Simons concludes that, "Apart from the observations given above few new similarities of taxonomic significance between the Pantodonta and other mammals have been observed and these are of such a general nature as to be inconclusive. From this negative point of view new emphasis is given to the distinctness of this order." He does, however, stress some of the resemblances to *Deltatherium*, a primitive mid-Paleocene creodont carnivore from North America and to certain condylarths such as *Periptychus* and *Phenacodus*. This is where the matter should be left because the interrelationships of these and other primitive placental mammal groups of the Paleocene are themselves poorly understood.

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JOURNAL OF PALEONTOLOGY, V. 35, NO. 3, P. 640–657, MAY, 1961

SOCIETY RECORDS AND ACTIVITIES

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A Late Cretaceous mammal from Dragon Canyon, Utah ..... *William A. Clemens* 578
Recent literature on Mesozoic ammonites, continued ..... *Otto Haas* 580
Pleistocene bighorn sheep from the Great Basin .. *Wm. Lee Stokes* and *Ken C. Condie* 598
Miocene Foraminifera from the Lajas Valley, southwest Puerto Rico .. *W. A. Gordon* 610
The supposed Pliocene Pebas beds of the Upper Juruá River, Brazil ..... *George Gaylord Simpson* 620
The genera *Microaulopora* Kuntz, 1895, and *Guembelina* Kuntz, 1895, and the status of *Guembelina* Egger, 1899 ..... *Alfred R. Loeblich, Jr.* and *Helen Tappan* 625

PALEONTOLOGICAL NOTES

Type specimens of North American Paleozoic Radiolaria ..... *William R. Riedel* and *Helen P. Foreman* 628
The lower dentition of *Proterix loomisi* Matthew? ..... *J. R. Macdonald* 632
Additional note on ovoviviparous *Turritella* ..... *Katherine V. W. Palmer* 633
Recently described birds and mammals from Cuban caves ..... *Pierce Brodkorb* 633

CORRECTION

Note on some species of Ostracoda described by A. M. Norman, a correction ..... *W. A. van den Bold* 636

NOTICES 637

REVIEW 638

SOCIETY RECORDS AND ACTIVITIES

Membership list of the Paleontological Society 640
Proposed new members 655